DATABASE ANALYISIS OF CORAL POPULATION DISTIBUTIONS IN THE CARIBBEAN REGION, 200 ka to PRESENT

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ABSTRACT

Concern for the future of coral reef ecosystems has motivated scientists to examine the fossil record to predict changes in coral distribution and population health. Specifically, in regions of concern, such as the Caribbean, a compilation of long-term records of coral reef health and biogeographic change during climate perturbations are can provide useful data for conservation efforts. The Caribbean coral reef record through the last 200,000 years (Pleistocene and Holocene) provides a good indicator of general reef construction. For this thesis, I have compiled a database of dominant reef corals across the Caribbean from 200 ka to present, which documents how species have been distributed over the last four sea level highs and their associated climatic changes. The presence and habitat of different coral species around the Caribbean and their changes over time can indicate both dominant morphological preferences and environmental controls on species distribution. Here, we found that the three main reef builders, *Acropora palmata, Acropora cervicornis*, and *Montastraea* "*annularis*", have distinct reef zonation and distribution throughout the Pleistocene and Holocene. Changes from these typical distributions, like a contraction of the *A. palmata* during the marine isotopic stage 5e (125,000 ka), show an influence of a cold, northern sea surface temperature and rapid sea level rise on *A. palmata* production. A species turnover from *Montastraea nanyci* to *M.* "*annularis*" reflects replacement during an extinction of *M. nanyci* around 82,000 ka. These changes in species ranges and reef location show the susceptibility of these *Monstastraea* to niche absences and morphological changes. The recent history of coral responses to sea-level and climatic change provides the best understanding for how reefs will adapt to future alterations in temperature and carbon dioxide levels and anthropogenic activity. Knowing what changes to expect in the composition and structure of reef ecosystems will be a critical tool to help prevent, or mitigate large-scale ecosystem collapse of coral reefs in the future.

Keywords: Holocene; Pleistocene; reef; climate change; *Acropora.*

INTRODUCTION

One of the greatest challenges facing our society today is planning for the effects of human impact on the environment. Within this challenge is the difficulty of planning for changes in modern coral reef ecosystems that support various uses from fishing to tourism. Because a human lifetime can only record small-scale fluctuations in coral ecosystems, the fossil record is a necessary analogue to identify long-term stability, biogeography, and reef health (Jackson, 1992). Looking at these modern reefs with a deep time perspective can assist in predicting modern coral response to climatic change. Specifically, this research will focus on the geographic distribution and ecological niches of dominant reef corals from past sea-level highs during the late Pleistocene to the Holocene; these past sea level rises can provide data to assess modern ecological shifts. A similar study was performed on the Pliocene-Pleistocene transition and species turnover (Klauss, 2003). The 2003 study found that ecological generalists and fast growing corals had a much better ability to survive rapid changes than species restricted to a specific environment.

Long-term assessments of coral populations emphasize how deep-time perspectives on species survival rates can provide background data for a more critical look at Holocene reef stressors and their effect on coral distributions. Although the Pliocene-Pleistocene study (Klauss, 2003) focused on survival rates, this Pleistocene-Holocene assesses coral survival and zonation changes and alterations through time. By looking at the coral population dynamics in the Caribbean during the Pleistocene-Holocene, species biogeography and niche utilization changes through time can be regionalized and constrained. Therefore, this study aims to discuss the distribution of key reef-building coral species across the Caribbean region (Fig. 1) during the late Pleistocene-Holocene (200 ka to present).

Figure 1. Map of the Caribbean. The study area surveyed includes the Caribbean, Florida, the Bahamas, Bermuda, and the Gulf of Mexico.

Previous research has concluded that specific coral species have a strong rate of survival and reestablishment in the Caribbean after climate change events in the Quaternary (Aronson, 2007). Across three geologically distinct islands, Curacao, Barbados, and San Andres, Aronson found that over 90 percent of the major constituent reef builders were the same throughout the Pleistocene. These main species were the *Montastraea "annularis"*, *Monstastraea nancyi*, *Diploria strigosa*, and the two main Acroporids, *Acropora palmata* and *Acropora cervicornis* (Fig. 2). Several studies indicate that the distribution of species in the Pleistocene is non-random, and that there is significant taxonomic uniformity over entire islands (Jackson, 1992; Pandolfi and Jackson, 2001; Klauss, 2003). This implies these corals have a resistance to ecological stressors and an ability to re-populate a niche following a significant environmental perturbation, such as the >100m sea level changes observed in the past 200 Kyr (Fig. 3) (Siddall et al. 2005). Therefore, compiling a database of the occurrence, abundance, and niche of the main species of

reef builders (Fig. 2) allows us to map more subtle changes that may have occurred during the last 200,000 years Additionally, it is hypothesized that wave energy and light availability control species location (Pandolfi and Jackson, 2001; Wellington, 1982; Rowan and Knowlton, 1995). This study also documents this niche utilization over time, and what aspects of the reef system control species preference for certain reef zones.

Figure 2: Corals featured in this study. A) *Montastraea annularis* (Boulder Star Coral), B) *Acropora palmata* (Elkhorn Coral), C) *Acropora cervicornis* (Staghorn Coral), and D) *Diploria strigosa* (Symmetrical Brain Coral).

METHODS

The study area of the Caribbean was chosen because there are relatively few Pleistocene/Holocene corals in the Caribbean, and this area has been widely affected in the past 30 years by coral stress (Hurricanes, rising sea-level, warming ocean temps). This persistence of a handful of coral species as the dominant reef builders over the past 200 ka allows a resolved image of coral distribution changes, and a comparison to the present day for some of the greatest challenges for modern corals. The study focuses specifically on the Pleistocene because these corals are still the dominant reef builders in the modern Caribbean. Because we are currently in a high stand (i.e. relatively high sea-level), any reefs that grew below the current sea level is under water. High stands (Yellow Stars in Fig. 3) represent areas where data collection is possible because these are terrestrial projects. This leads to most data coming from 125 ka where the sea level exceeded that of the present by ~10 meters.

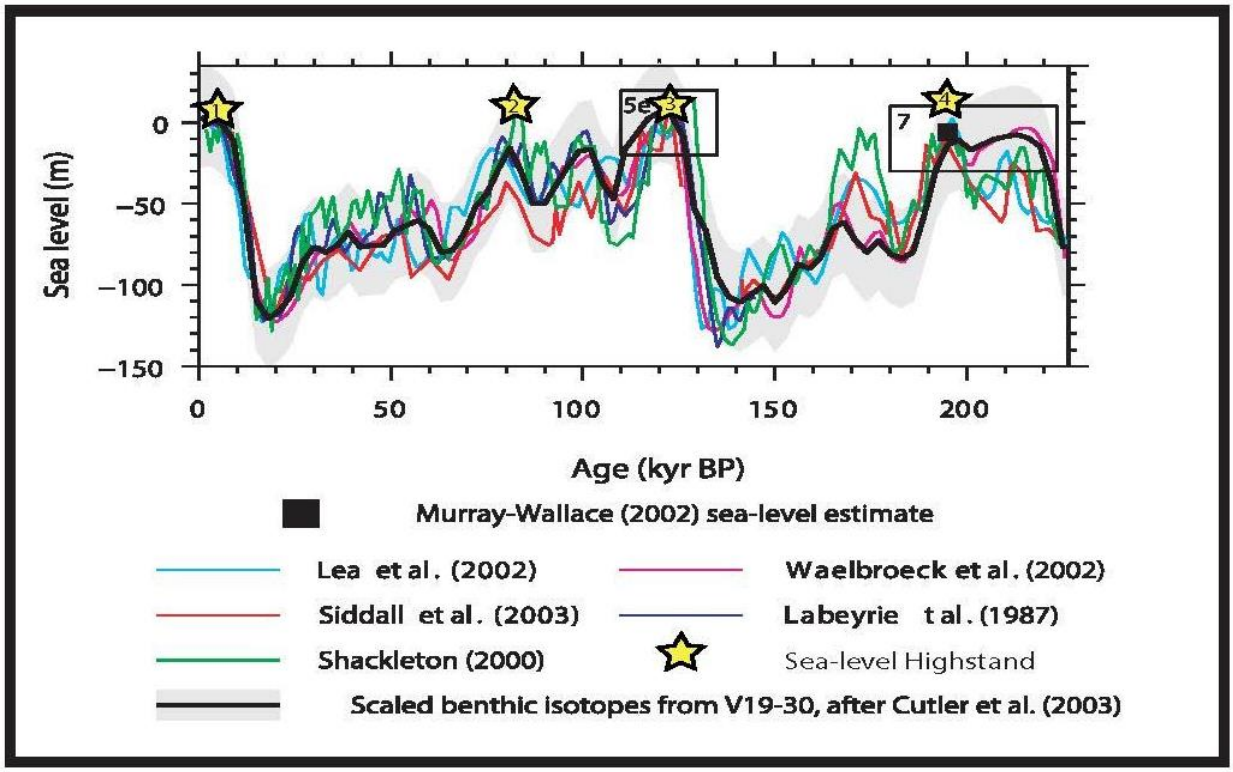


Figure 3. Sea-level heights over the past 230 ka; modified from Siddall et al. (2005). Stars indicate intervals where fossil reefs are preserved in the Caribbean during a sea-level high stand.

To build the Caribbean database (see Appendix A), a comprehensive literature survey was conducted; 48 scientific papers contained data on coral species occurrence, abundance, and niche utilization (i.e. location of the reef) during the late Pleistocene and Holocene (i.e., 200 ka to present). Note that not all time intervals have data for each location (Table 1). For each paper the country or region of the reef being assessed was recorded (e.g. Mexico, Belize, Dominican Republic). In addition to the generalized location, a more descriptive "secondary location" was also noted; which provides more specific information on where the reef complex was located (e.g. Enriquillo Valley, Isla Perez, Rendezvous Hill).

Coral genus and species names were recorded from each location and time interval. Although all species reported were added to the database, special attention was paid to the notably abundant corals of Aronson (2007); *Montastraea "annularis"*, *Monstastraea nancyi*, *Diploria strigosa*, *Acropora palmata* and *Acropora cervicornis*. The geological epoch for each occurrence was also defined as middle or late Pleistocene, or Holocene. The most common dates for the Pleistocene reefs were ~200 Kyr, ~125 Kyr, and ~82 Kyr. These time slices for the Pleistocene were expected as they correspond to the sea-level highstands (Fig. 2). Data from marine isotope stage 5e (MIS 5e) (125 Kyr) was the most common because this was the highest and sea level (Fig. 3). The present sea level high (MIS 1) restricts data acquisition from other times where the sea level was lower than present day, as these records can only be accessed by submarine coring. The Holocene fossil reef data are mostly from the past 100 years, but some recent drill-cores and minor sea-level fluctuations provide data from the past 10,000 years due (Hubbard, 2008; Mann, 1984). In addition, some regions have non-traditional Holocene and Pleistocene data due to tectonic isolation of reef zones. The Dominican Republic is unique because tectonic activity isolated a Holocene reef complex from the ocean, which lead to preservation of a mid-Holocene reef. Other special cases include Barbados, which experienced

tectonic uplift and has data recorded for all sea-level highs in the Pleistocene (Fig. 3) (Pandolfi and Jackson, 2001).

The zone on the reef was also recorded for each coral species. The basis for reef location was based on Jeremy Jackson's 1992 study on Pleistocene coral reef community structure; Jackson used the Barbados islands as examples and created generalized fringing reef zones (Figure 3). This 1992 study divided the reef into 4 zones based around the height on the reef and general morphology of a fringing reef complex. These general reef zones are also consistent terminology across many Caribbean reef studies. These zones were as follows: back reef (shoreward of reef crest, generally lagoonal, ranging from 0-10 meters depth), reef crest (zone of highest wave energy, 0-5 meters depth), upper fore reef (highest zone on the seaward slope of the reef, 5-15 meters depth, and lower fore reef (lowest part of the coral dominant zone on the seaward reef slope, 15-25 meters depth) (Fig. 4) (Jackson, 1992). The reef zones of *A. palmata, A. cervicornis, M. "annularis", M. nancyi,* and *D. strigosa* were recorded for each location in the database based on reef depth and reef shape. The generalized Pleistocene and Holocene Caribbean reef is depicted in Figure 4. By documenting the reef zone of corals, changes in

species dominance in particular niches can be resolved over many thousands of years.

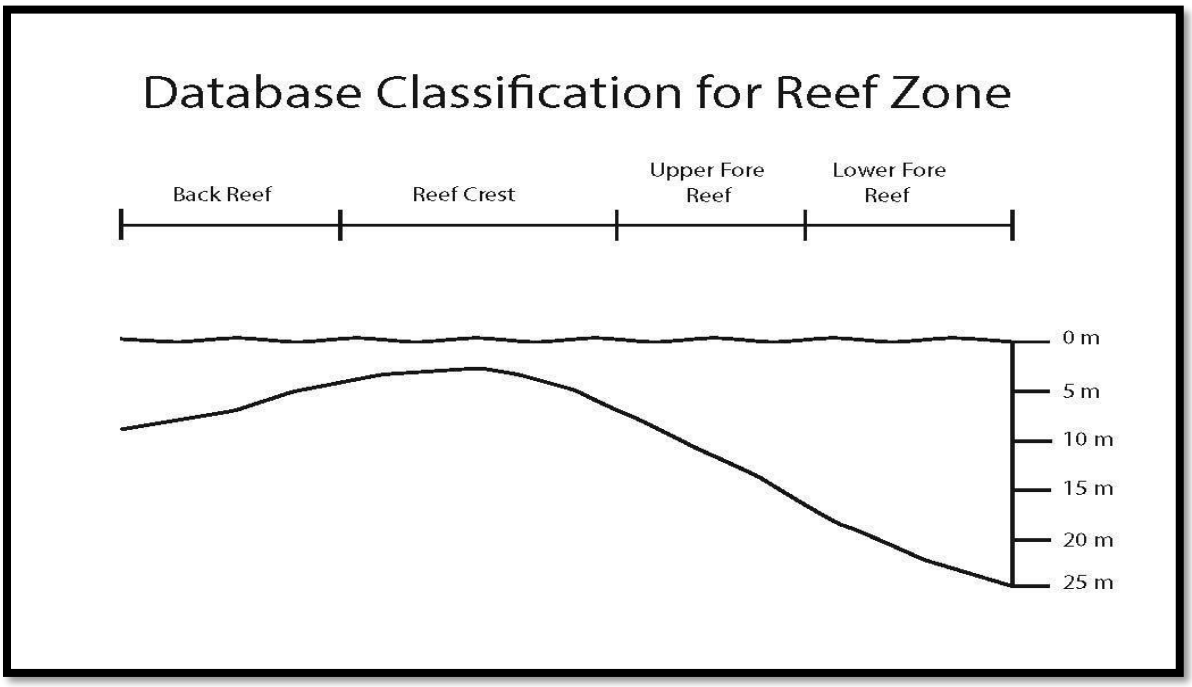


Figure 4. Classification scheme for reef zones used in this study

The "Percent Cover" of a particular coral species was also recorded in the database. exclusive (>90%), dominant (40-90%), frequent (30-40%), present (20-30%), low (<10%) and absent (0%) were used to categorize the species involvement in their particular reef zone. A distinction was made between areas with no data (i.e. no publications from that area or time interval) and a confirmed absence of a particular coral type. This allows for a clear appearance or disappearance of specific coral types over the observed time interval rather than a paucity of research or academic papers.

Once this database was made, I took these categorical classifications of coral presence in a particular reef zone and created quantitative values. This allowed the data to be better analyzed through multivariate analysis. The categorical terms listed above (exclusive, dominant, frequent, present, low, and absent) were give values five to zero with five being exclusive and zero being none. These were

The multivariate statistical analysis was run over the database. First, I converted the numerical percent cover data to relative abundances. Then, I square-root transformed the values to deemphasize the dominant species. Then, I did a Bray-Curtis similarity measure to create a resemblance matrix. Next, I performed a cluster analysis with a similarity profile test (SIMPROF). This defined the biofacies. To tell which taxa dominated each biofacies, I performed a similarity percentage routine (SIMPER). To visualize the data, the data was plotted using a non-metric multidimensional scaling ordination. This all followed the methods of Clarke & Gorley (2006) using Primer v6 software.

RESULTS

The five main dominant reef-building corals species provide a record of changing niche utilization by reef zonation. The generalized reef zonation pattern involving *A. palmata, A. cervicornis, Montastraea,* and *D. strigosa* gives the best baseline from which to judge the changes in reef patterns. This pattern can change through the various sea-level changes of the Pleistocene and could help with responding to niche absences like the loss of *A. palmata* from the reef crest in the modern.

In general, the reef crest zone was dominated by *A. palmata*; this coral species is constrained to 0-5 m from the surface where its fast growth and resistance to waves gave it a necessary advantage in its restricted zone (Montaggioni et al., 2009). Findings from Jackson in Barbados and Jamaica (Jackson, 2007) align with the findings of the database which shows a distinct domination of the reef crest by *A. palmata* at most locations in the Caribbean during the Pleistocene and Holocene (Fig. 5). By creating these generalized cross-sections, each reef can be compared to the average to find out how and why it varies.

Figure 5 shows the distributions of the five dominant corals in this database. *A. palmata* shows the characteristic dominance of the reef crest down to around five meters. The crest has a few sparse occurrences of *Montastraea* spp. and *A. cervicornis*. The *A. cervicornis* showed the strongest presence in the upper fore reef, while the *M. "annularis"* tended to dominate the lower fore reef beyond 10-15 meters. The *M. nancyi*, which went extinct after 82 kyr to the present had a similar zone to the *M. "annularis"* on the lower fore reef; however, the *M. nancyi* was larger and slightly more dominant, especially in the back reef.

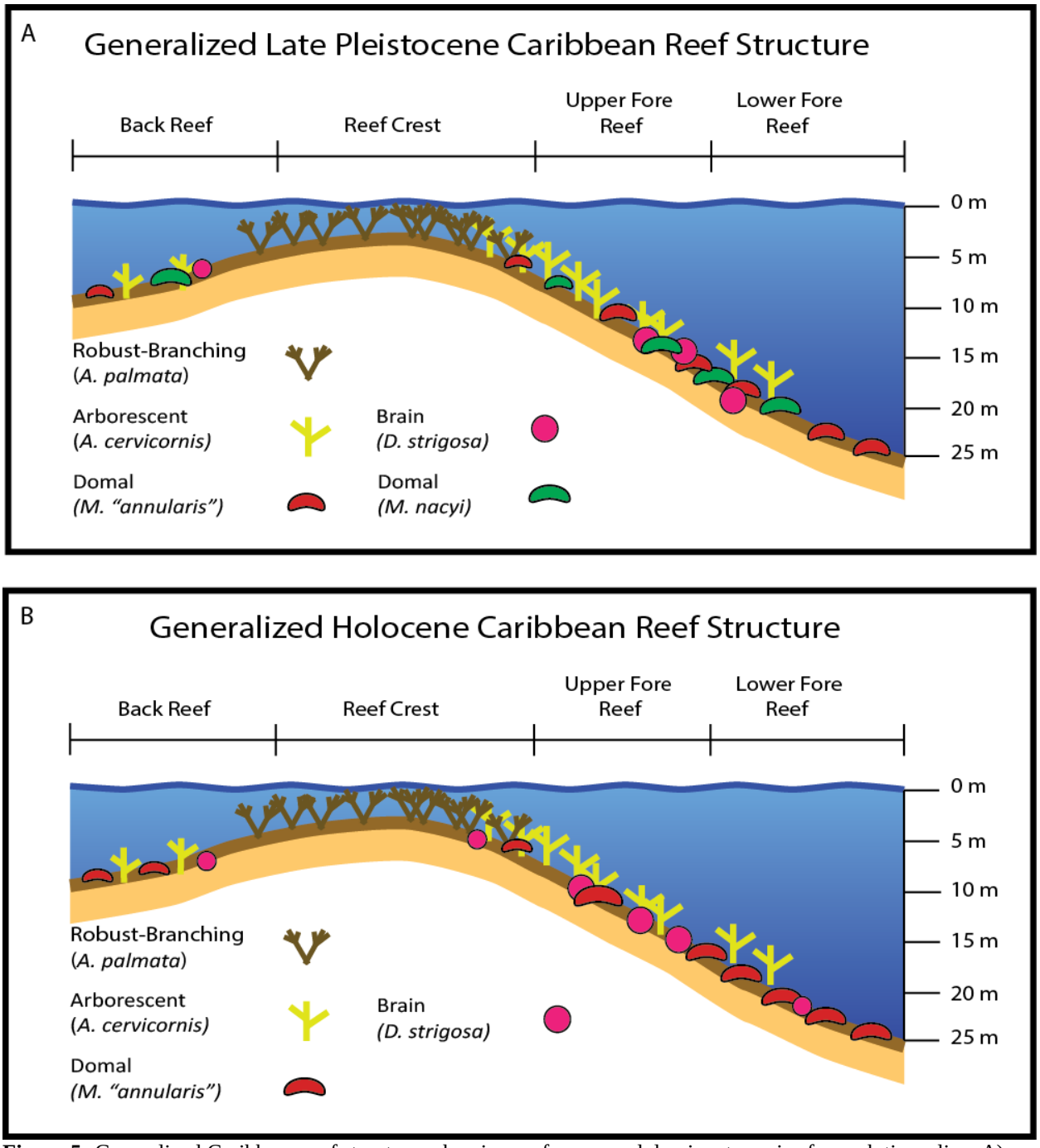


Figure 5: Generalized Caribbean reef structures showing reef zones and dominant species for each time slice. A) Late Pleistocene B) Holocene. Size of the icons indicates shrinking of the species when they are in the back reef or pushing their zone boundaries.

Occurrence of *Acropora palmata* (Elkhorn coral)

Pleistocene:

The *A. palmata* data generated one of the most revealing findings of the paleobiogeographic coral maps. In the Pleistocene (125 kyr), *A. palmata* had a limited presence in the northern Caribbean (Fig. 6a). There were recorded absences on both the South east Florida shelf margin and islands in the Northern Bahamas. Along with theses *A. palmata* absences, the database also recorded a low percent cover, when compared to the Holocene distribution; (Fig. 6b), for other northern regions (e.g. Isla Perez, East Yucatan). In general, during the Pleistocene, *A. palmata* had a high percent cover on the reef crest, but in some of the more northern reefs there was a reduction in cover. These decreased abundances in percent cover were noted in the three main northern research sites: the Florida Keys, southern Bahamas, and Eastern Mexico. The absence of data in Cuba limits the extent of observation for the northern distribution of *A. palmata* as the main reef crest stony coral.

Further south, *A. palmata* displays dominance on the reef crest and a strong presence on the upper fore reef. *A. palmata* even exhibits exclusive cover along several research sites in Guadeloupe and Barbados. The niche monopoloy of the *A. palmata* in the Antilles and Hispaniola contrasts the relative low abundance in the northern Caribbean.

Holocene:

Acropora palmata shows a similar, yet more expanded geographic distribution in the Holocene (Fig. 6b) when compared with the late Pleistocene (Fig. 6a). North of the Caribbean, there is a noted absence of *A. palmata* in Bermuda; this is the only noted absence of *A. palmata* in the Holocene (NOAA). *A. palmata* is also present in the Flower Gardens marine area in the

Gulf of Mexico. In addition, *A. palmata* shows dominant cover in the East Yucatan area and around the peninsula toward Isla Perez, in contrast to the lower percent cover observed in this area at 125 kyr.

Along the SE Florida shelf margin and the southern Bahamas, *A. palmata* exhibits exclusive percent cover on the reef crest. This is in contrasts to the low percent cover that was observed at 125 kyr. The Florida Keys also exhibit an increase in percent cover over the past 125 thousand years. In the northern Bahamas, we see the appearance of *A. palmata* in the record where it was previously absent (Fig. 6).

In the regions where there was strong dominance of *A. palmata* at 125 kyr, there remains remarkable stability in the abundance of *A. palmata*. Barbados and Guadeloupe both still have exclusive percent cover of this species on the reef crest. Similarly, in Hispaniola and other parts of the Antilles island chain, *A. palmata* retains its dominance on the reef. There is a slight reduction in percent cover in southern Jamaica. The appearance of Cuban data supports the dominance of *A. palmata* for Holocene Caribbean reefs.

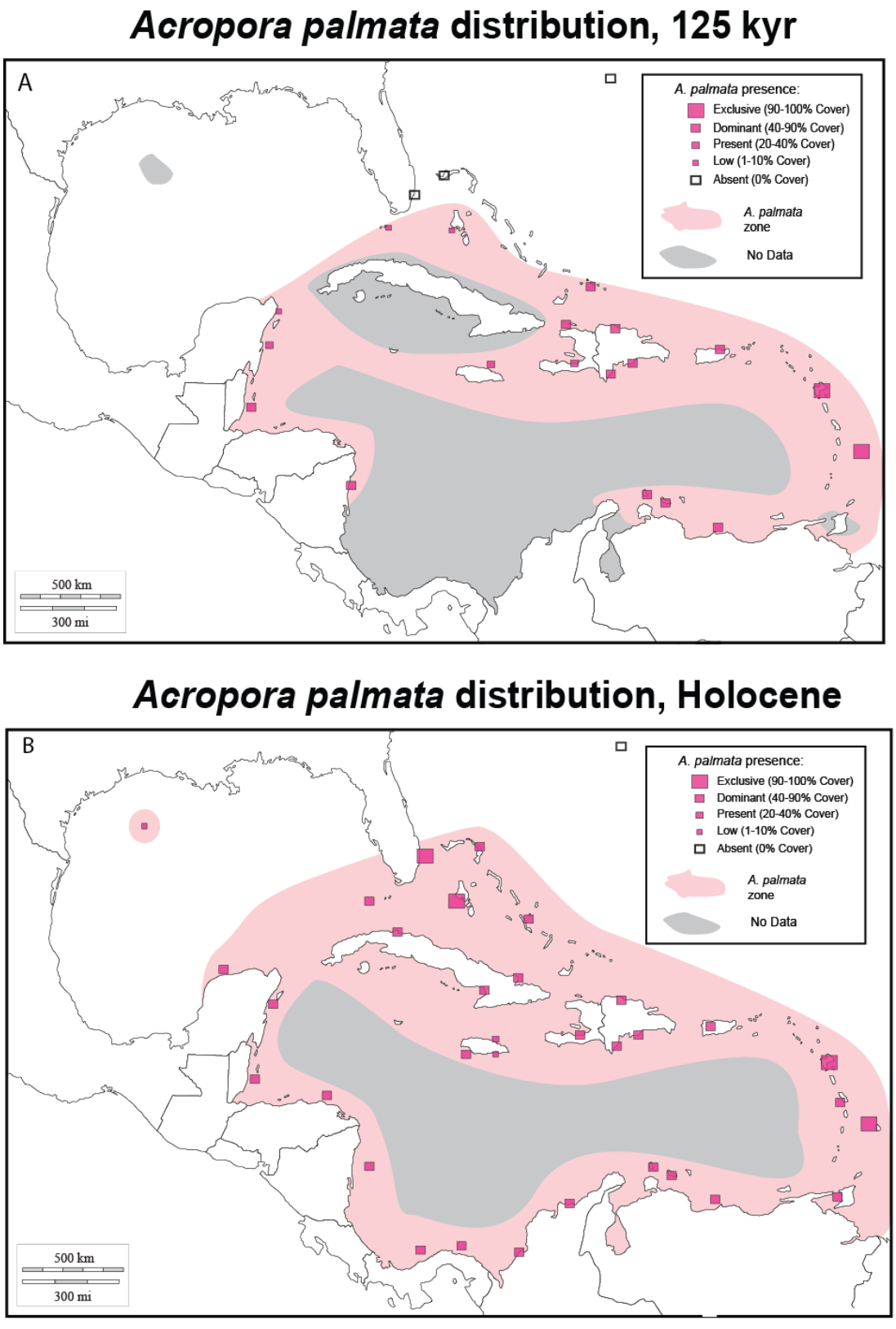


Figure 6: Acropora palmata distribution in the Caribbean A) Late Pleistocene B) Holocene. Note the absence of A. palmata in Florida at 125 kyr, then the exclusive domination in the Holocene.

Occurrence of *Acropora cervicornis* (Staghorn coral)

Pleistocene:

The *Acropora cervicornis* data (Fig. 7a) display similar zonal trends to the *A. palmata* (Fig. 6a). At 125 kyr, *A. cervicornis* shows low to present percent cover in the northern Caribbean (northern and southern Bahamas as well as the Florida Keys). However, on the SE Florida shelf margin, *A. cervicornis* shows a dominant percent cover on the upper fore reef. This close geographic relationship, but drastically different percent cover is an interesting contrast. The lower percent cover continues to be present in the east Yucatan area of Mexico. The absence of Cuban Pleistocene data again restricts the ability to constrain the northern distributions of *A. cervicornis* around 125 ka.

Across other areas of the Caribbean, such as the southern Caribbean, there is a clear dominance of *A. cervicornis* on the upper fore reef and lower crest across all recorded reefs. The database noted multiple Pleistocene reefs in Barbados that had exclusive *A. cervicornis* cover in the upper fore reef zone (Jackson, 2001). This exclusive cover was found mostly just out of the depth range of the *A. palmata* areas, which characterize the reef crest or shallowest areas of the reef.

Holocene:

As with the *A. palmata*, the *A. cervicornis* record (Fig. 7b) exhibits remarkable similarity across the middle Pleistocene into the Holocene. The percent cover in the upper fore reef zone stays the same from the Pleistocene to the Holocene in all Lesser Antilles islands and through the southern Caribbean Sea. The Dominican Republic experienced an increase in *A. cervicornis* abundance with two of the sites transitioning from dominant to exclusive cover on areas the

upper fore reef.

In the northern parts of the Caribbean, such as the Bahamas, the Florida shelf, and Florida Keys, the percent cover of *A. cervicornis* showed an increase from mostly low or present at 125 ka to dominant or exclusive in the Holocene (Fig. 7b). Along the western edge of the Caribbean, the barrier island chain in Belize exhibited an increase in percent cover along with areas further north in the Eastern Yucatan peninsula.

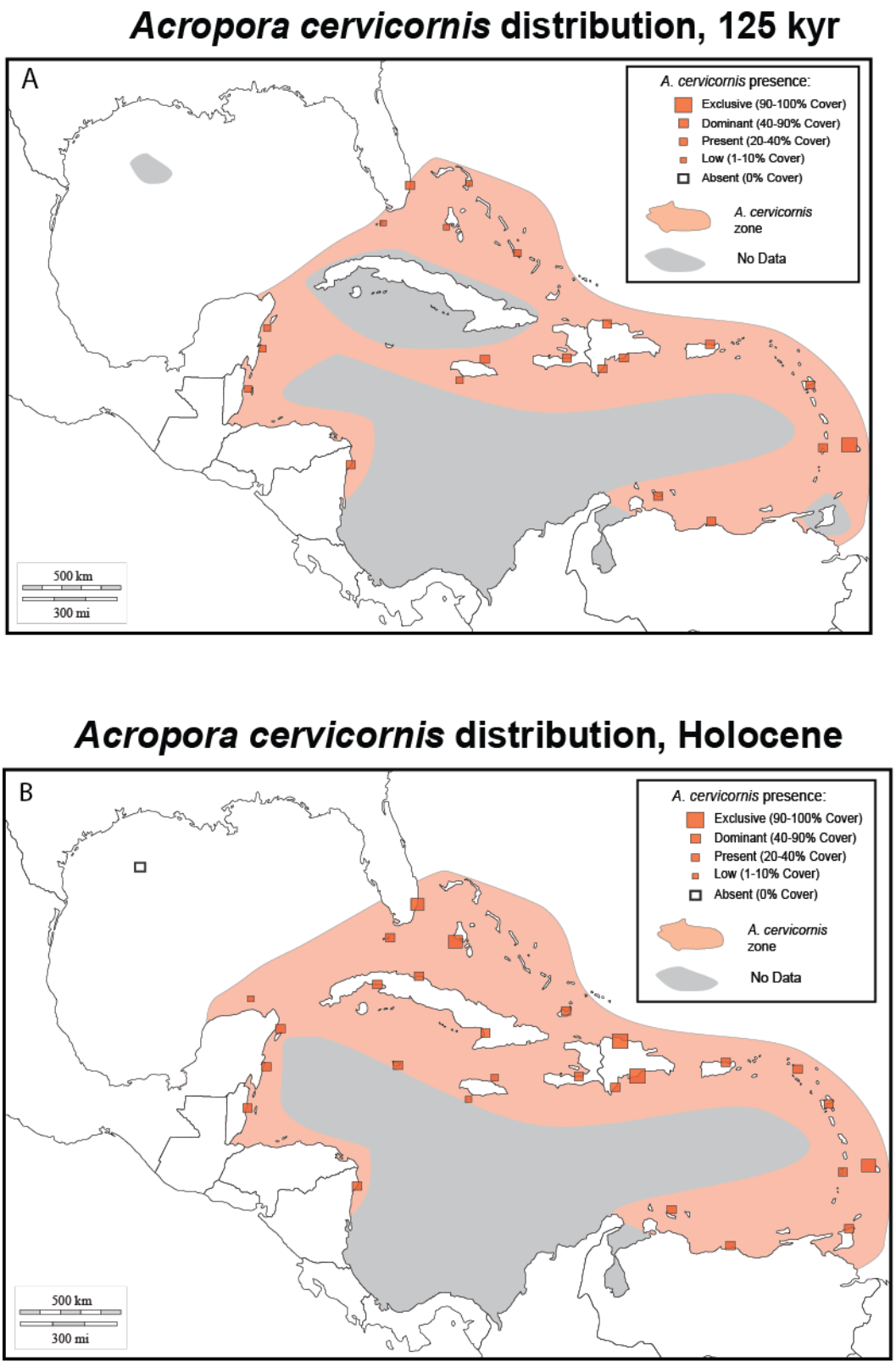


Figure 7. *Acropora cervicornis* distribution data plotted across the Caribbean. A) Late Pleistocene B) Holocene. Note the increase in percent cover in the northern Caribbean region from the Pleistocene to the Holocene.

Occurrence of *Montastraea "annularis"* and *M. nancyi* (Boulder Star Coral and Organ-Pipe)

Pleistocene:

The *Montastraea* data (Fig. 8) includes both *M. "annularis"* and *M. nancyi* because these were booth dominant reef builders during the Pleistocene. Both *Montastraea* show a widespread distribution in the Caribbean for the 125 kyr time interval. The southern limits of *Montastraea* extend as far south as Panama and as far north as Bermuda (Fig. 8a). *M. nancyi* and *M. "annularis"* exist in tandem across the reefs in the Pleistocene. The *M. nancyi* frequently exhibits percent cover that exceeds that of the *M. "annularis"* (indicated by larger size squares) also in the graphs of percent cover (Fig. 10). When they are both present on a reef system, *M. nancyi* typically has greater abundance across the upper and lower reef slope. It should be noted that *M. nancyi* goes extinct at the MIS 5a (82 kyr) according to the last appearance in Barbados (Pandolfi, 2007).

Holocene:

In the modern, the *M. nancyi* has gone extinct leaving only *M. "annularis"* and *M. cavernosa* as the remaining *Montastraea* species. For the purposes of reef building potential and percent cover, only the *M. "annularis"* locations and percent covers have been included in the Holocene map. The *M. "annularis"* exhibits an increase in percent cover across many locations in the Caribbean; in Barbados, the *M. "annularis"* increases from present to exclusive in two areas surveyed. A similar record occurs in the Bahamas where there is an increase in cover taken up by the *M. "annularis".* Although no data exists for the Pleistocene Flower Gardens, in the Holocene, *M. "annularis"* is a present reef builder in that marine area.

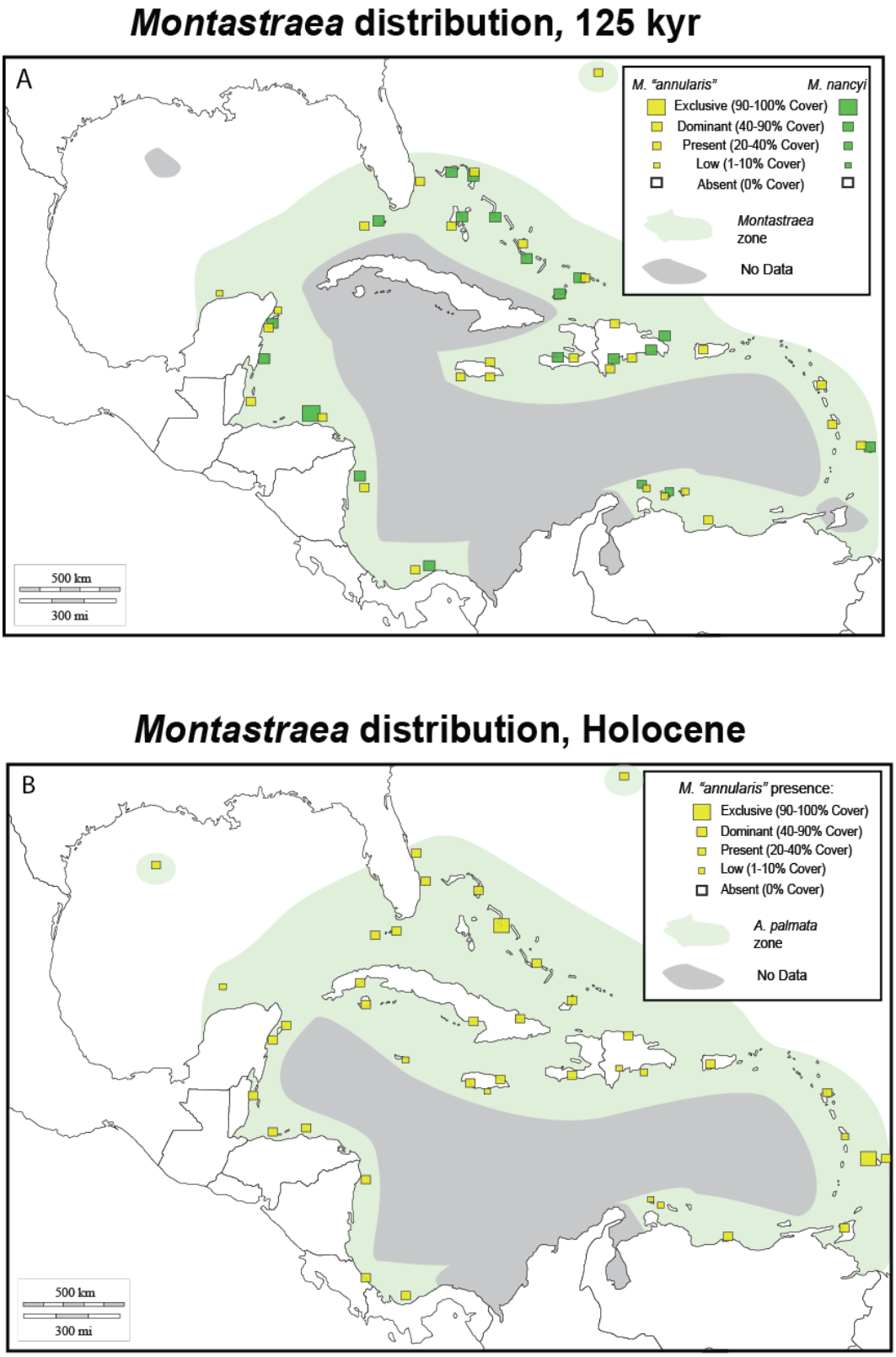


Figure 8. *Montastraea* distribution data plotted across the Caribbean. A) Late Pleistocene B) Holocene. For the 125 kyr map, notice the overlap in almost every location between the two corals.

Occurrence of *Diploria strigosa* (Symmetrical Brain Coral)

Pleistocene:

The *D. strigosa* data (Figure 9) display what would seem to be typical coral geographic dispersion around the Caribbean, ranging from Venezuela up to the Southeast Florida coast and Bermuda. A few reef locations, one in the Dominican Republic and one in Barbados, had recorded absences of *D. strigosa* however, the predominant percent cover across Caribbean Pleistocene reefs was "dominant", and was mostly observed in the upper parts of the lower fore reef and the lower parts of the upper fore reef (10-20 m). A few occurrences of *D. strigosa* are present in the back reef also.

Holocene:

D. strigosa continues to have a strong presence in Caribbean reefs from the Pleistocene into the Holocene, and maintains its geographic distribution (Fig. 9b). This region of typical distribution is along the coasts in the reefal areas of the Caribbean tropics. While less dominant than the other reef builders, *D. strigosa* maintains a very stable distribution. There are a few occurrences of *D. strigosa* higher up on the fore reef and on the reef crest in Curacao. This represents a slight movement up the fore reef from the Pleistocene.

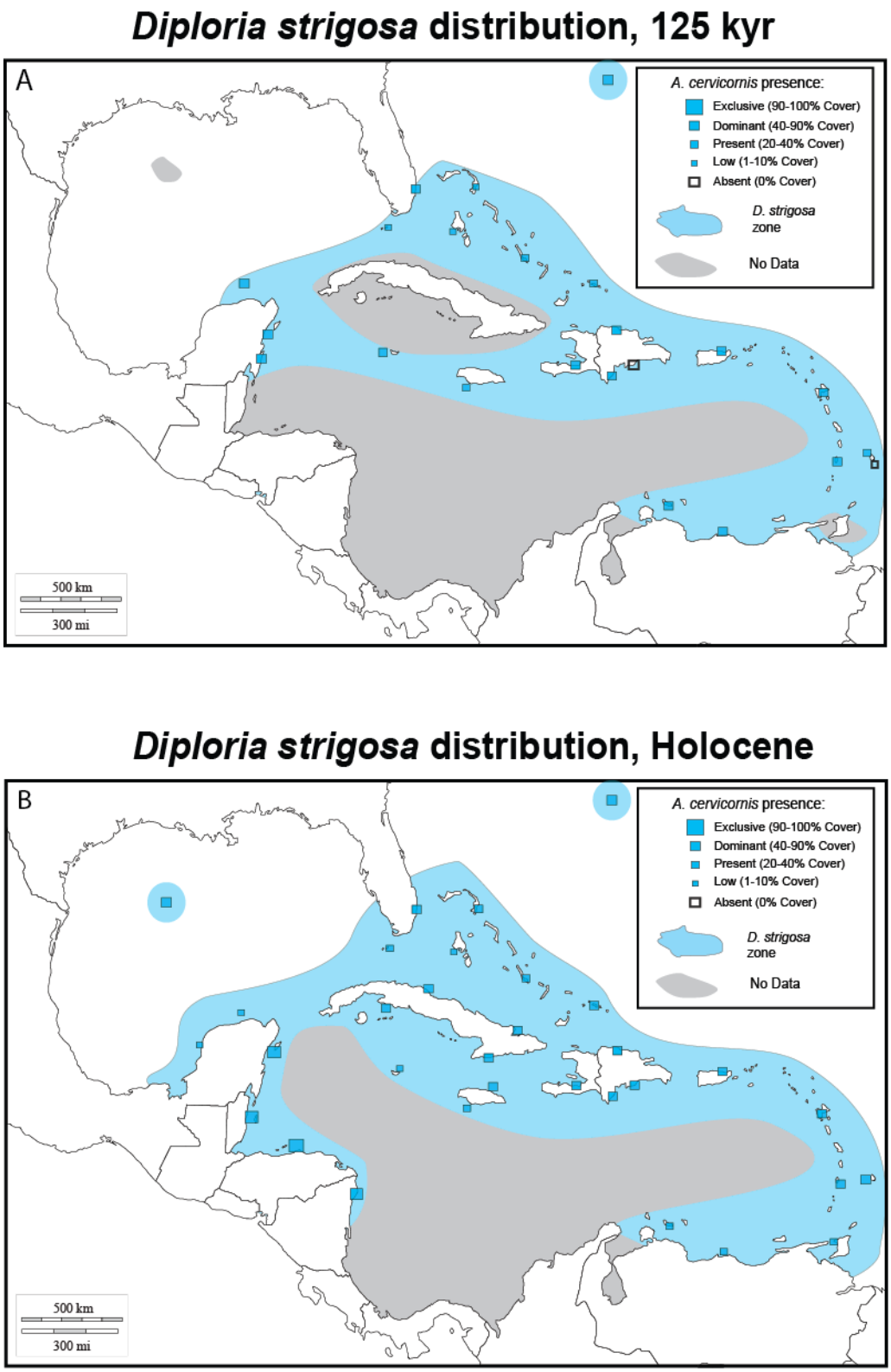


Figure 9: *Diploria strigosa* distribution data plotted across the Caribbean. A) Late Pleistocene B) Holocene.

Figure 10 displays in graph form what the maps represent across five regions in the Caribbean. The breakdown of the regions was selected based on geographic location in the Caribbean (Supplementary Data 2). Each percent cover value listed in the methods section was applied a numerical value. 5 for exclusive, 4 for dominant, 3 for frequent, 2 for present, 1 for low, and 0 for absent. Then these numbers were totaled and averaged for the five Caribbean zones (e.g. Florida/Bermuda/Bahamas, Lesser Antilles etc.). This gives a quantitative measure of changes in percent cover across the studied time interval in each region.

The values are mostly consistent thorough the time surveyed. Two notable exceptions are the increase in percent cover for *M. "annularis"* in four out of the five reef zones. This shows that the *M. "annualaris"* is expanding from the Pleistocene to Holocene. Also, there is an evident change in *A. palmata* in the Florida region from Pleistocene to Holocene from an average low percent cover to exclusive.

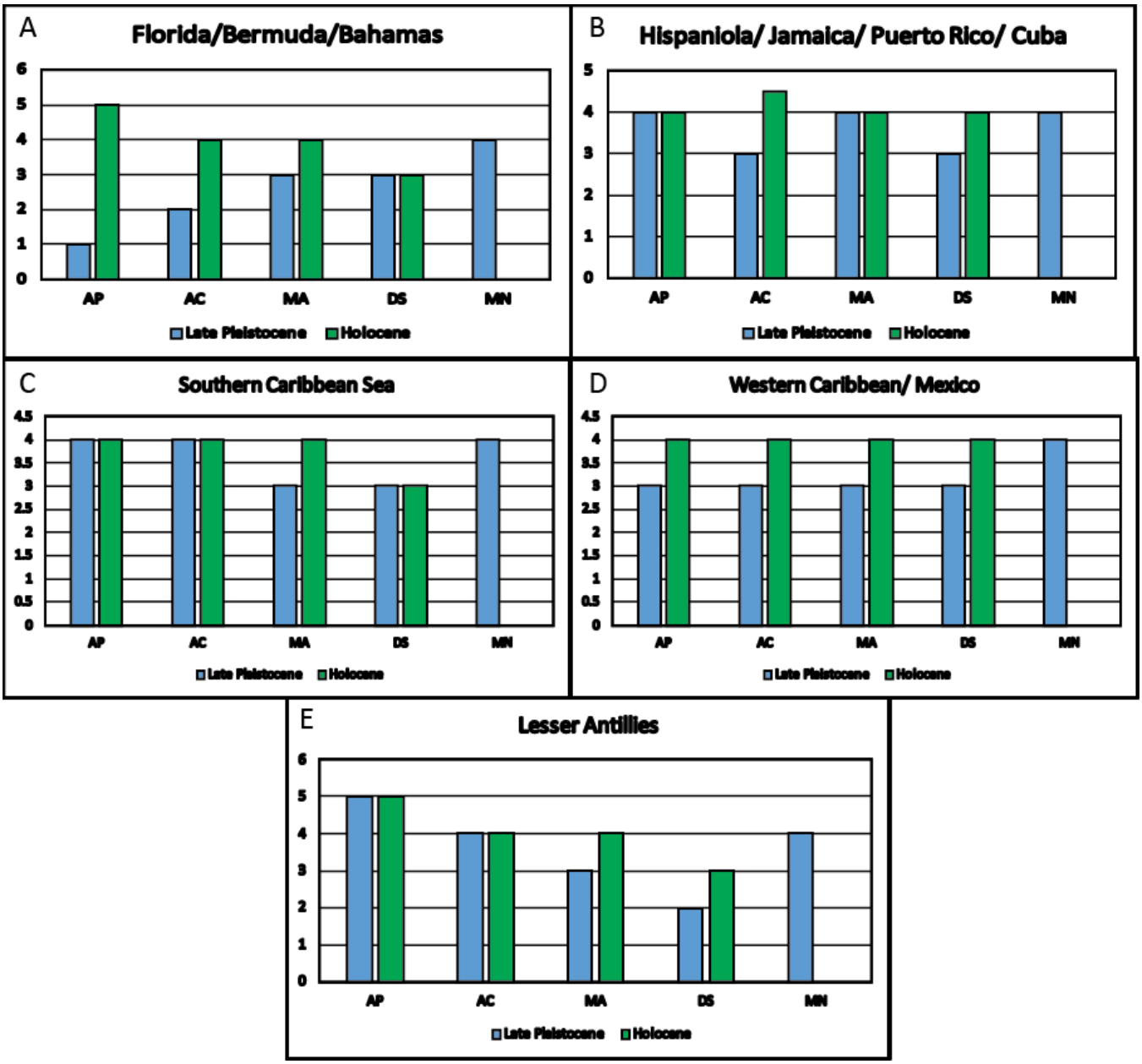


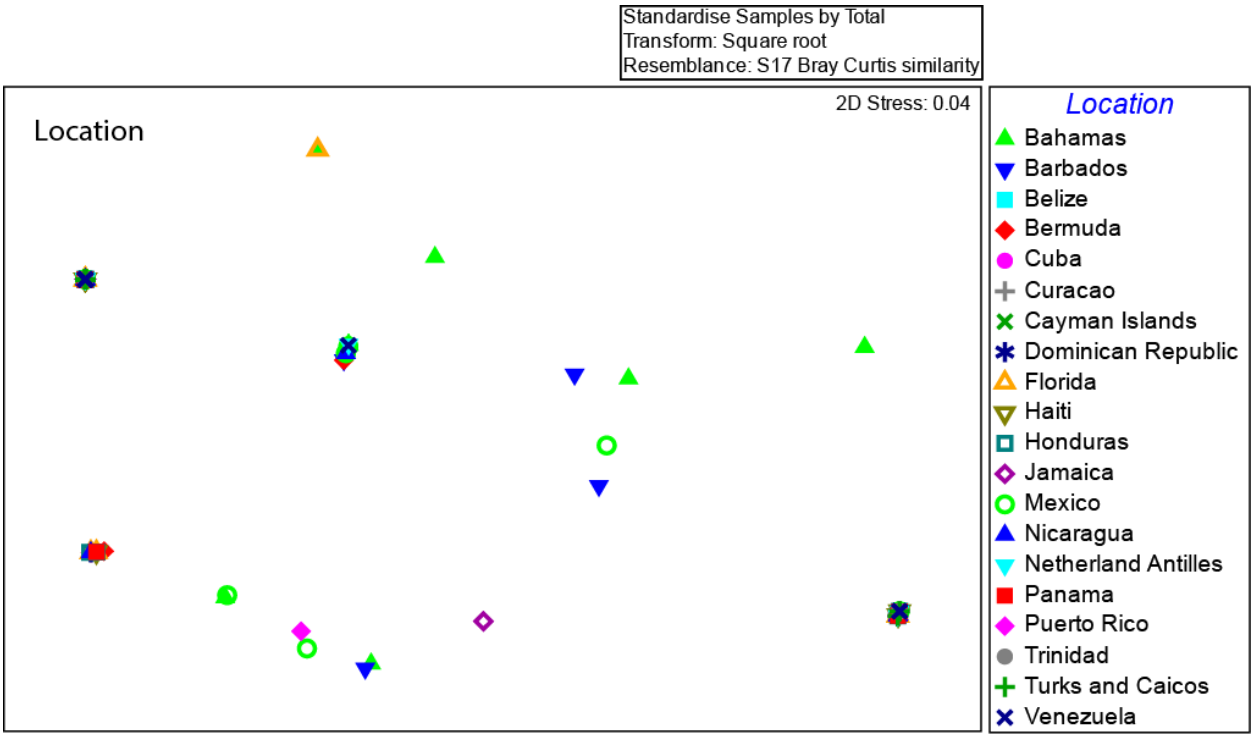
Figure 10: Graphs comparing percent cover of the 5 main reef building corals from the Pleistocene to the Holocene in 5 reef zones in the Caribbean. AP= *A. palmata*, AC= *A. cervicornis*, MA= *M. "annularis"*, DS= *D. strigosa*, and MN= *M. nancyi*.

Multivariate Analysis:

Figure 11 shows the non-metric multidimensional analysis of the database of Caribbean coral database. The graph that shows the plot of the Reef Zone shows a strong preference of *A. palmata* on the crest of the reef. This can be seen in the clustering of blue triangles all correlated with the *Acropora palmata*. The other corals show less preference for reef zone with a relatively random scatter between the Back Reef, Upper Fore, and Lower Fore. *M. nancyi* shows a preference toward the Upper Fore and Back Reef.

For the plot of the Age, *M. nancyi* shows a strong presence in the Late Pleistocene. The other four corals do not show any preference for the age whether it be Late Pleistocene or Holocene. The final scatter plot of Location shows very little correlation with location and coral type. There is a noted overlap of Bahamas and Florida in the upper center of the plot. The rest of the points plot quite randomly showing little relationship between location and sample preference.

The samples from this database do have strong similarity from the Late Pleistocene into the Holocene.



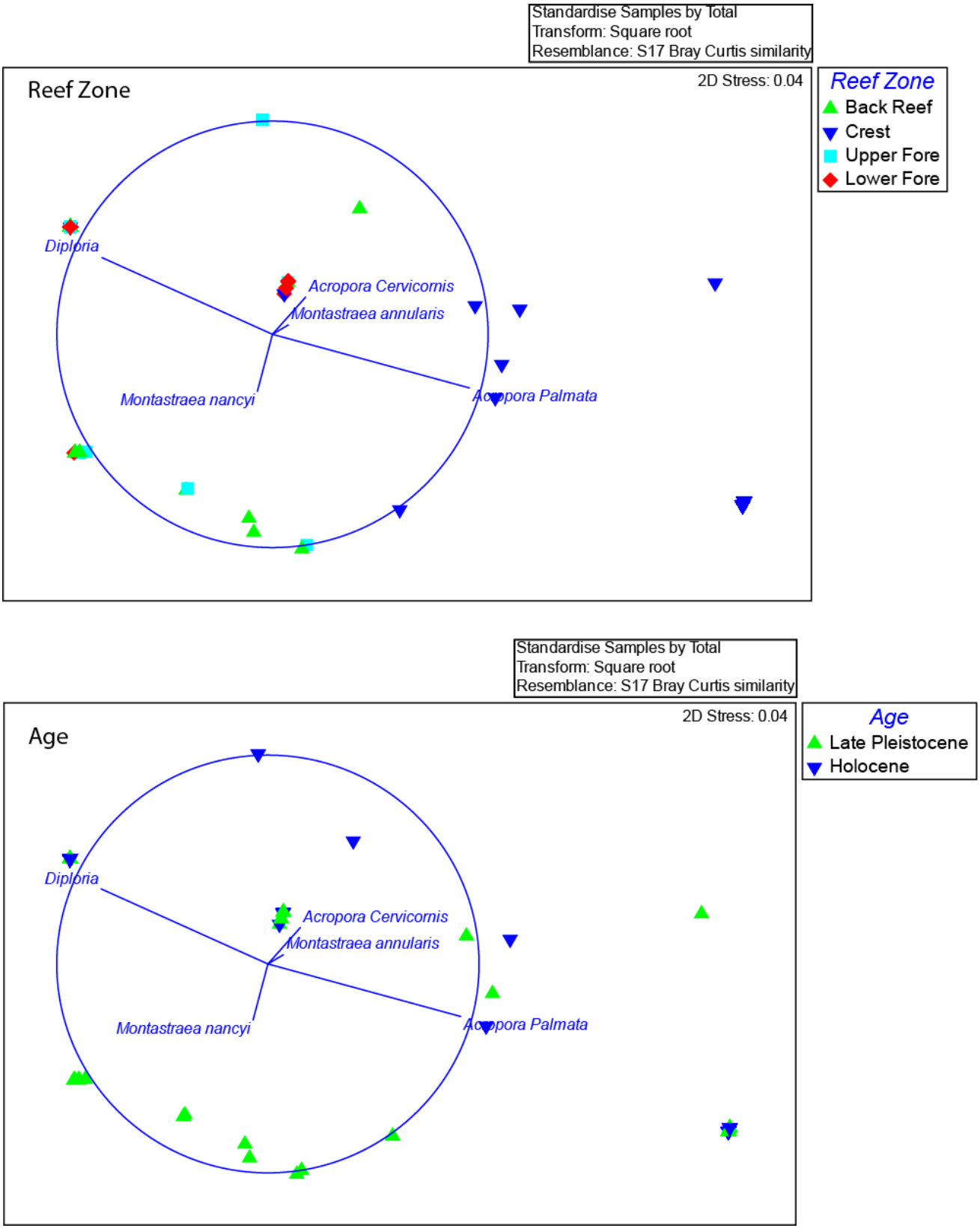


Figure 11: Non-metric multidimensional plot of Location, Reef Zone, and Age from the Caribbean Coral Database

DISCUSSION

This study found a very consistent biogeographic distribution of main reef building corals in the Caribbean. This implies a long term stability of these corals even through the large sea-level fluctuations of the Pleistocene. Major discussion points include the extinction of *M. nancyi*, the expansion of *M. "annularis"* into this vacant *M. nancyi* niche, and range shifts and modern challenges to Acroporids in the Caribbean.

The range shifts in the Acroporid distribution from 200 ka to the Holocene have several potential explanations. The northward expansion of *A. palmata* in the last 125 kyrs could first be the result of a phenomenon known as the inimical waters (Precht and Miller, 2007). These inimical waters or harmful waters are caused by tidal influence and can lead to weakened or terminated coral growth. Inimical waters can occur in areas where there is large tidal influence and impact. This can result in periodic wetting and drying in addition to the influx of sediment from the flood plain. These changes on the monthly scale significantly harm coral growth rates (Manzello, 2015). Although this is theorized for the Pleistocene, it may provide insight into the modern reefs (Precht and Miller, 2007) as sea-level fluctuates and tides reach different areas. Manzello recorded the effect of these inimical waters on coral growth in the Florida Keys, and found that constant influx of Florida Bay water and the temperature fluctuations from tidal influence all negatively affected the calcification and extension rate of the corals. This could have been what was happening in the Late Pleistocene that affected *Acropora* growth. Since Acroporids are shallow-water corals, they can be proportionally more affected by tidal changes. The higher sea-level recorded at 125 kyr could change the influence of tides, and increase tidal impact on islands. This would be especially important in the Florida Bay and Bahamas where their low relief reefs could be impacted by tides, exposing the large fringing reef crest and back reef.

Precht and Miller (2007) observed a similar *Acropora* distribution with the absence of both *A. cervicornis* and *A. palmata* in Key Largo during the middle Pleistocene. They theorized this absence to be the response of the *Acropora* to low sea surface temperatures in the winter. Because *Acropora* corals are often found in shallow water (NOAA), they are susceptible to ocean temperature changes in the top part of the water column. Temperatures in these shallow ocean zones are influenced by air temperature (USGS). Since *Acropora* species and other corals have a narrow band of temperatures that they thrive in, shifts out of these ranges can harm coral growth.

Both the cold winter water and inimical waters theories for *Acropora* absence in the north Caribbean during the Late Pleistocene can mutually exist. Sea-surface temperature in combination with variable tidal flooding and exposure can lead to reduced coral growth and poor conditions. In addition to temperature changes, sediment flux from tidal movement can affect coral skeletal density (Manzello, 2015).

The maps of *Montastraea* distributions (Fig. 8) do not show any clear trends in terms of range expansion or contraction over the last 120 kyr. However, it does reveal that after the extinction of *M. nancyi* (Fig. 8, 10), there was a complete takeover of *M. "annularis"*, in particular on the back reef and upper fore reef zone (Fig. 5,8,10). The *M. nancyi* primarily occurred in these zones prior to 82,000 ka. Along with this niche shift, the *M. "annularis"* complex increased in colony size and percent cover to fill in the vacated niche left by *M. nancyi* (Fig. 5,8,10). Prada et al. 2016 found that the increased availability of shallow water environment after 82 kyr, followed by the extinction of *M. nancyi*, allowed for the expansion and domination of *M. "annularis"* during this recent interglacial. This supports a competition hypothesis articulated by Pandolfi and Jackson (2001) that suggests that these two groups were competing for resources and space on the reef slope. Nevertheless, if they were competing for

the same niche with similar morphologies, what caused *M. nancyi* to go extinct while *M. "annularis"* thrived? One hypothesis could be that the differentiated *M. "annularis"* had the ability to recruit different algae symbionts that were better adapted to changing climate conditions (Rowan and Knowlton, 1995). This genetic variation and expansion gives hope for *Montastraea* corals response to climate change today and in the future.

Another result that is worth discussing is the definition of *Montastraea "annularis".* Knowlton et al. (1996) discovered that *M. annularis* was actually a species complex of three morphologically similar species of these 1-25 meter depth mound corals. Initially they were believed to be a hybrid, but the study conducted in Panama found differences in their reproductive timing that would limit hybridization among the species. The *M. annularis* complex was divided after this discovery into *M. franksi*, *M. faveolata*, and *M. annularis* sensu stricto (Knowlton et al. 1996). Because of this relatively recent differentiation, species distinctions before 1996 are nearly impossible. Budd et al. (2004) noted, however, that even though these three species of the *M. annularis* complex overlap, their occupied reef zone (i.e. the depth at which they are most abundant) varies. *M. faveolata* and *M. annularis* have their highest abundance in the 0-3 m and 3-6 m zones of the reef front, respectively, while *M. franksi* has its highest abundance in the 12-15 m zone (Fig. 5, 11). This distribution on the reef, although less distinct in the Bahamas and Dominican Republic, is found throughout the Caribbean in Curacao, Barbados, and much of the Southern Caribbean (Budd, 2004). This distribution is seen in the Pleistocene through the Holocene with the exception of the *M. nancyi*, whose extinction at 82 kyr led to niche replacement by the columnar *M. annularis* s.s. (Budd et al., 2004; Pandolfi et al. 2002).

Discussion of Multivariate Analysis:

First, to address the Fig. 11 Age plot, this makes sense with the literature that *M. nancyi* would have its main presence and influence in the Late Pleistocene. *M. nancyi's* extinction at 82 kyr precludes it from being a reef builder in the Holocene.

Second, the Fig. 11 Reef Zone, shows a distinct dominance and presence of the A. palmata on the reef crest. This makes sense with the biology of A. palmata, and its ability to exist in the high wave energy and high light zones. This water movement allows it to survive and thrive in the areas of the reef with large amounts of water movement. There is a slight preference for *M. annularis* when *M. nancyi* is not dominant. This shows the zonal change toward *M. annularis* upon the extinction of *M. nancyi* in the Holocene time.

Third, the plot of Location in the Caribbean shows no trends based on the plot. Each reef location does, however, plot in large clusters. This shows that there is uniformity across the Late Pleistocene into the Holocene. This reaffirms the hypothesis proposed by the coral maps, which show an incredible maintenance of coral biogeography even through the large sea-level and climactic changes of the past 200 kyr.

Discussion of the Database:

The lack of differentiation between the *M. "annularis"* species complex before the 1995 discovery is an interesting area for future research. The species complex has three distinct members and the repetition of population biogeography and niche utilization studies with this three species distinction could provide more nuanced understanding of climatic responses over the past 200 ka (Fig. 12). Particularly, the *M. franksi* species tends to dominate lower reef zones, so it could be used as an indicator of a deeper reef facies (Weil and Knowlton, 1994). Furthermore, Pandolfi and Jackson (2001) found that, in Curacao, *M. faveolata* and *M. annularis*

s.s. occupied very different locations on the reef in the Pleistocene. The *M. faveolata* was found on the back reef with no appearance on the reef crest (Pandolfi and Jackson, 2001). Further research that separates this complex could provide more resolution about the ecological changes within the *Montastraea* genus over time.

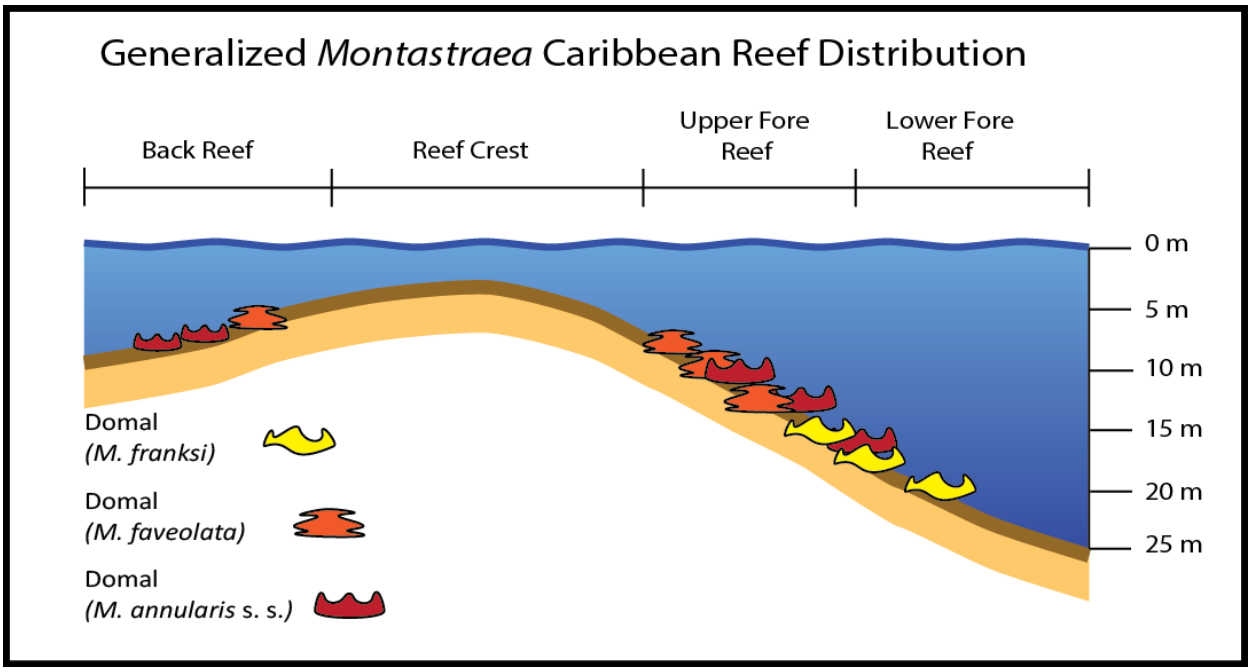


Figure 12: Distribution of the differentiated *M. "annularis"* species complex.

Another comment on the database is what time periods had accessible data. Data from the Marine Isotopic State 7 (MIS 7) interglacial period of the middle Pleistocene (195 kyr) and the MIS 5a from the late Pleistocene (82 kyr) were limited (see Table 1). This paucity of data is a product of the current sea level highstand. Because the sea level is currently at a near high point for the last 200 kyr, coral data from 195 and 82 ka are underwater and harder to access. For localities where there is data from these intervals, like Barbados, there are comprehensive studies of reefs in these areas (Pandolfi and Jackson, 2006). Barbados was affected by uplift during the Pleistocene, which helps provide a more complete picture of the Pleistocene reef structure. Although data for 125 kyr are abundant and presented in this study, information on the transition from 195-125 or 125-82 could help highlight more changes in species distribution and the

specific response of corals to global warming and cooling.

One limitation of the database was the consideration of reef style. While most reefs considered in this study were fringing reefs, the differentiation between fringing and patch reefs might highlight changes in coral domination and percent cover. In addition to these reef consideration, the angle of the reef slope could have a large control on the impact of sea-level rise. An example of this would be in lower angle reef slopes, like the Bahamas, a one-meter sea-level rise would result in a greater lateral movement inland, whereas an island like Barbados, where the reef slope has a high angle would not. This could change the tidal influence and have a particular impact on reef crest species, like *A. palmata*, that might experience more variable environmental conditions.

Another aspect of the database information that is worth noting is the occurrence of *A. prolifera* (see Supplemental Appendix A). This species is believed to be a hybridization between *A. cervicornis* and *A. palmata* (Vollmer et al. 2002; Oppen et al. 2000). *A. prolifera* occurs at the Crest - Upper Fore Reef boundary, which substantiates this theory as this is the cross over point between the *A. palmata* dominated crest, and the *A. cervicornis* dominated upper fore reef. This species of *Acropora* was not included in this study because the hybrid is only of minor importance to Pleistocene-Holocene reef building, and all of these *Acropora* corals are equally impacted in the post-1980's Caribbean reefs, to which I turn now.

CARIBBEAN REEF THREATS

Planning for the future of corals and their response to climatic shifts is one of the main goals of coral scientists. As mentioned earlier, studies with long-term perspectives can provide insight that is unable to be studied in a human life time (Connell and Sousa, 1983). While there are some sites, like Discovery Bay in Jamaica, where there have been long standing research sights, most sites fail to capture a multi-decadal picture of the reef and its changes. This leaves the fossil record as the only window into the past. This long- term view helps with broad species responses, but in the short term, it can be useful to look at the interplay of factors that affect Caribbean reefs and their interactions with one another. These threats listed below provide a way to assess modern corals, and how they will be pressured under expected climatic changes.

Looking into the modern and future trends toward more algal dominated reefs could be good focus for the fossil record. The taphonomic preference toward stony corals could be obscuring short-term events of coral mass mortality, algal proliferation, and coral recovery (Aronson and Precht, 1997). This is short-term resolution is of current importance with White Band Disease, the die-off of *Diadema antillarum*, and a period of intense hurricane activity decreasing *A. cervicornis* levels from around 70% to nearly 0% from 1970s to 1980s. (Aronson and Precht, 2001). With *A. cervicornis* and *A. palmata* at a significant low, macroalgae have taken over this niche in most reef systems (Aronson and Precht, 1997; Greenstein et al. 1998). This drastically changes the reef ecosystem. While some reefs have already restored their Acroporids, some still lack these main reef builders (Aronson and Precht, 2001), and *Acropora* rebound could take many human lifetimes, or may never even occur. Because we cannot know whether corals will return, the fossil record can serve as our only analog to predict coral responses. We can look for these short term coral absences in the fossil record to garner percent cover evidence on past mass mortalities and rebounds. Figure 13 shows the current state of

Acroporids. Although the range is seemingly abundant, on the individual reef scale, the loss of 60-90% *Acropora* cover can have major impact, including leaving rubble on the reef, which can negatively affect future coral recruitment (Aronson an Precht, 2001). These secondary impacts are an additional fear of modern conservationists.

Figure 13: NOAA Atlantic Acropora Coral Fact Sheet

If we use the Pleistocene as the analog for the modern, coral populations seem to be relatively stable across hundreds of thousands of years. Interestingly, the climatic fluctuations in the Pleistocene have as extreme magnitudes as some climate change models predict (Araujo et al. 2005); however, the current trend is toward a warming climate not a cooling one. While corals do respond poorly to anomalously cold weather (Lirman, 2011), even small warming results in temperature pressure and bleaching (Precht and Miller, 2007). And even if the Pleistocene-Holocene corals looked at in this study can handle the extreme climate and sea level fluctuations projected, there will be a large difference in the pace of environmental changes and the added impact of human activity such as fishing and land cover changes (Pandolfi and Jackson, 2006; Knowlton, 2001). The coral system is one the most dynamic in the world, and

these ecosystems are adaptable to various changes in their environment, so continually monitored responses to stimuli like algal blooms and disease will yield greater resolution on how coral react to stressors.

1. Disease

White band disease is a bacterial coral disease that affects *Acropora* corals in the Caribbean. This disease only influences two of the primary reef builders, *A. palmata* and *A. cervicornis*, and leads to the rapid death of coral tissue. This disease has also been studied in reference to ocean temperature, and the effect of WBD has been shown to increase with rising ocean temperature (Randall, 2014). This current issue has been a major catalyst for reef collapse.

White pox disease is similar to White band disease and causes necrosis of coral tissue. It effects *A. palmata* and result in the white-pox affected area to be colonized by turf algae (Patterson, 2002). There are other diseases such as Black band disease and Yellow-band disease that can affect all the reef builders including *D. strigosa* and *M. annularis*.

2. Overfishing and *Diadema antillarum*

During the mid-1980s, there was a significant hit to coral stability in the Caribbean. This event did not affect the coral directly like White Band Disease, but resulted in the reduction of algal grazing on Caribbean reefs, which suffocated living corals. This event was the mass mortality of *Diadema antillarum*, a long-spine urchin species, which experienced more than 97% elimination. These urchins are primary grazers on reefs in the Caribbean; with this urchin mortality in 1983, algal overgrowth on reefs became common (Crabbe, 2016). Without grazing of algal growth, Algal overgrowth stops living corals from receiving light and nutrients from the surrounding water .A 15-year-long study performed in Jamaica found that the area where the *D. antillarum* had returned had an increase in *A. cervicornis* of 26 percent cover compared to no *A.*

cervicornis return in an adjacent reef with sparse to no *D. antillarum* (Crabbe, 2016). This was after a 2005 mass bleaching event and shows the importance that one herbivore can have on the stability of a coral state.

This *D. antillarum* issue in conjunction with a reduction in grazing by herbivores like parrotfish due to overfishing makes for a two-pronged attack on a coral stable state (Knowlton, 1992). This stable state hypothesis was further expanded on in a later study that modeled the effect of different grazers on the stable state of Caribbean reefs. Mumby et al. (2007) found that the combination of urchins and parrotfish grazing algae on at least 42% of the reef every 6 months results in a high probability that the reef will remain above the unstable equilibrium (Fig. 14). This means that if parrot fish continue to get overfished, there is a higher likelihood of an algae dominated reef.

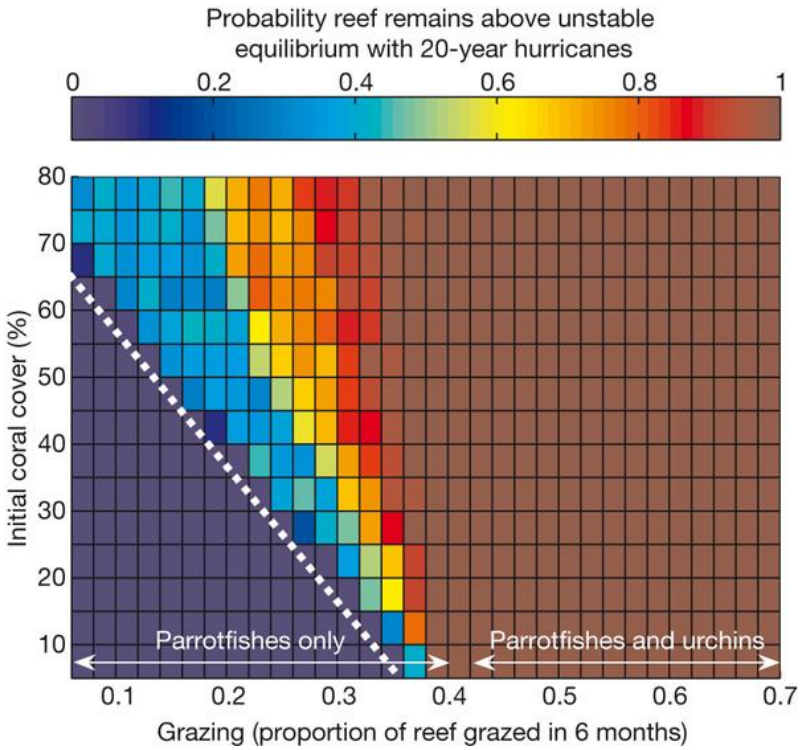


Figure 14: Probability that a reef remains above an unstable equilibrium (Mumby, 2007). Note that as percent of the reef grazed increases, the likelihood of coral stable state increases.

3. CO_2 Rise, aragonite saturations, and Surface Warming

With the onset of industrialization, humans have been utilizing fossil fuels for their easy and efficient access to energy; however, this form of energy releases CO_2 into the atmosphere during combustion. The feedback cycle for CO_2 entering the atmosphere is complex, but certain impacts of an increasing atmospheric concentration are more predictable. In addition to increasing concentration, the rate of CO_2 input into the atmosphere has a control on how extremely corals will be effected (Honisch, 2012). Figure 15b shows that at a higher rate of CO_2 increase (red line), the pH has a more extreme response than a slower rate and this results in a more acidic ocean. Fig. 15c shows that the same rapid doubling of CO_2 results in a decrease in the saturation of aragonite, which is a necessary constituent for corals to build their skeletons. In conclusion, the faster the CO_2 doubles, the less time the ocean has to stabilize the carbon dioxide concentration, and the more likely that corals will be pushed beyond their ideal growth environments. Some climate models also predict that temperatures sufficient to induce bleaching could become annual events within a few decades (Knowlton, 2001).

Coral bleaching caused by raising surface temperatures has resulted in the loss of 19% of the world's coral reefs (Glynn, 1992). As the greenhouse gas emissions continue, this is modeled to increase temperatures and result in more bleaching (DeCarlo, 2016). While a 2^{o} C increases in ocean temperature is said to avoid the most extreme impacts of climate change (Conference of Parties 21st), a study done by DeCarlo in the South China Sea showed that while ocean temperatures in the open ocean can vary by 2 degrees, micro climatic effects like reduced wind, current, and anomalous pressure systems can cause areas like the reef flat to increase in temperature by ~6^{o} C (DeCarlo, 2016). Temperature changes like these can result in mass bleaching, especially in the back reef and reef crest. On deeper parts of the reef, like the upper fore reef, this study found that around 7 m below the surface, bottom water cooled corals on the

fore reef, which kept bleaching from occurring. To bring this back to our Caribbean corals, this would mean intense temperature stress for the *Acroporids*, while the *D. strigosa* and *M. "annularis*" would avoid these intense seasonal temperature effects.

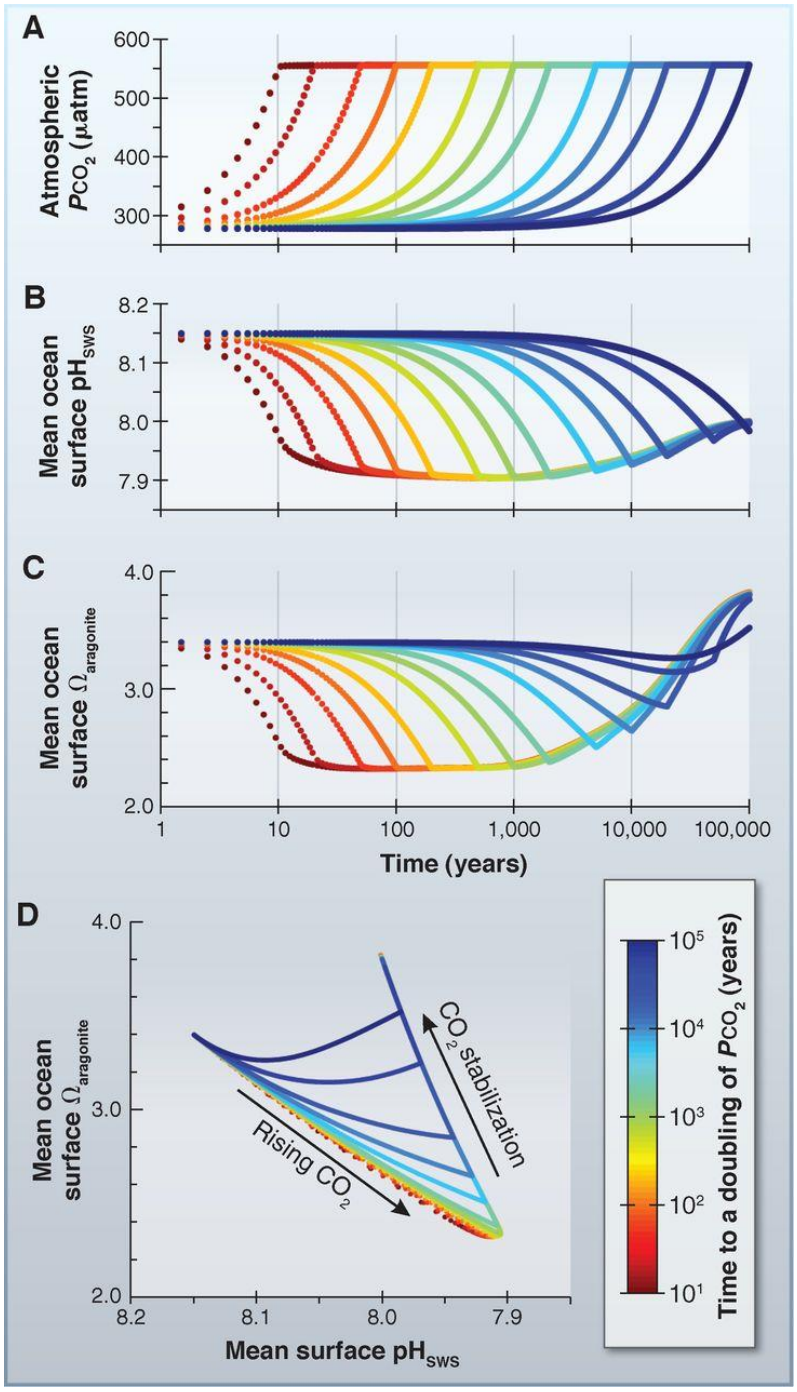


Figure 15: Graph relating rate of CO_2 increase, Ocean surface pH, and Aragonite Saturation (Honisch, 2012). Red lines represent rapid rate of CO_2 doubling; Blue lines represent a slower rate of CO_2 doubling. Note how the faster rate (Red Line) allows less CO_2 stabilization to occur, which forces pH lower and Aragonite saturation down.

4. Hope for Coral Reefs

Although the future for Caribbean corals looks bleak, there are a few factors that paint a less grim picture for these essential reefs. First, after bleaching events corals can re-recruit zooxanthellae. Not only this, but there have been cases where certain corals can recruit different types of symbionts, and this diversity of symbiotic algal relationships allows corals to adapt to changes in the environment, like warming or salinity (Knowlton, 2001). In addition, corals can exhibit local adaptation on the molecular level, which can help bleaching response and environmental stress response (Kenkel and Matz, 2016).

CONCLUSIONS

1. Across the Pleistocene and Holocene in the Caribbean, corals tend to maintain their geographic distribution.
2. There is a predictable zonation of Pleistocene corals along the reef that is determined by growth rate, wave energy, and light. Since this community structure has persisted across multiple phases of global climate change, variations from this structure indicate other factors at play, such as human factors.
3. Variations in the geographic ranges of the dominant Pleistocene reef building corals can provide insight into how corals will respond to future atmospheric and sea-water changes.
4. *M. "annularis"* corals ability to repopulate the niche left by the *M. nancyi* shows a versatility of corals across reef zones, and *Montastraea's* unique ability to differentiate and utilize those new niches.
5. Caribbean reefs are at a period of high stress because of the confluence of hurricanes, grazer mortality, and *Acropora* diseases. Along with these issues, there are also more long-term trends like CO_2 entering the atmosphere that will change the environment for Caribbean corals. Considering the implications of these changes and attempting to mitigate future degradation will benefit local populations, tourism, and marine life.

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REFERENCES

Araujo, MB, RG Pearson, W. Thuiller, and M. Erhard. 2005. "Validation of Species-Climate Impact Models under Climate Change." Global Change Biology 11 (9): 1504–13. doi:10.1111/j.1365-2486.2005.001000.x.

Aronson, Richard B., and William F. Precht. 1997. "Stasis, Biological Disturbance, and Community Structure of a Holocene Coral Reef." Paleobiology 23 (3): 326–46.

Aronson, Richard B., and William F. Precht. 2001. "White-Band Disease and the Changing Face of Caribbean Coral Reefs." Hydrobiologia 460 (1): 25–38. doi:10.1023/A:1013103928980.

———. 2000. "Herbivory and Algal Dynamics on the Coral Reef at Discovery Bay, Jamaica." Limnology and Oceanography 45 (1): 251–55. doi:10.4319/lo.2000.45.1.0251.

Austermann, J., JX Mitrovica, K. Latychev, and GA Milne. 2013. "Barbados-Based Estimate of Ice Volume at Last Glacial Maximum Affected by Subducted Plate." Nature Geoscience 6 (7): 553–57. doi:10.1038/NGEO1859.

Blanchon, P. 2010. "Reef Demise and Back-Stepping during the Last Interglacial, Northeast Yucatan." Coral Reefs 29 (2): 481–98. doi:10.1007/s00338-010-0599-0.

Blanchon, Paul, and Anton Eisenhauer. 2000. "Multi-Stage Reef Development on Barbados during the Last Interglaciation." Quaternary Science Reviews 20 (10): 1093–1112. doi:10.1016/S0277-3791(00)00173-6.

Braithwaite, C. J. R., L. F. Montaggioni, G. F. Camoin, H. Dalmasso, W. C. Dullo, and A. Mangini. 2000. "Origins and Development of Holocene Coral Reefs: A Revisited Model Based on Reef Boreholes in the Seychelles, Indian Ocean." International Journal of Earth Sciences 89 (2): 431–45. doi:10.1007/s005310000078.

Budd, Ann F., and John M. Pandolfi. 2004. "Overlapping Species Boundaries and Hybridization within the Montastraea 'annularis' Reef Coral Complex in the Pleistocene of the Bahama Islands." Paleobiology 30 (3): 396–425.

Connell, Joseph H., and Wayne P. Sousa. 1983. "On the Evidence Needed to Judge Ecological Stability or Persistence." The American Naturalist 121 (6): 789–824.

Crabbe, M. (2016) Comparison of Two Reef Sites on the North Coast of Jamaica over a 15-Year Period. American Journal of Climate Change, 5, 2-7. doi: 10.4236/ajcc.2016.51002.

DeCarlo, Thomas M., Anne L. Cohen, George T. F. Wong, Kristen A. Davis, Pat Lohmann, and Keryea Soong. 2017. "Mass Coral Mortality under Local Amplification of 2 °C Ocean Warming." *Scientific Reports* 7 (March): 44586.

Dodge, RE, RG Fairbanks, LK Benninger, and F. Maurrasse. 1983. "Pleistocene Sea Levels from Raised Coral Reefs of Haiti." Science (Washington) 218 (4591): 1423–25.

Dumas, Bernard, Chi Trach Hoang, and Jeannine Raffy. 2006. "Record of MIS 5 Sea-Level Highstands Based on U/Th Dated Coral Terraces of Haiti." Quaternary International 145 (Journal Article): 106–18. doi:10.1016/j.quaint.2005.07.010.

Fairbanks, R. 1978. "The Marine Oxygen Isotope Record in Pleistocene Coral, Barbados, West Indies1." Quaternary Research 10 (2): 181–96. doi:10.1016/0033-5894(78)90100-X.

Feuillet, N., P. Tapponnier, I. Manighetti, B. Villemant, and G. C. P. King. 2004. "Differential Uplift and Tilt of Pleistocene Reef Platforms and Quaternary Slip Rate on the Morne-Piton Normal Fault (Guadeloupe, French West Indies)." Journal of Geophysical Research - Solid Earth 109 (B2): B02404–n/a. doi:10.1029/2003JB002496.

Gallup, Christina D., H. Cheng, F. W. Taylor, and R. L. Edwards. 2002. "Direct Determination of the Timing of Sea Level Change during Termination II." Science 295 (5553): 310–13. doi:10.1126/science.1065494.

Geological Approaches to Coral Reef Ecology: Ecological Studies, 192. 2007. Book, Whole. DE: Springer Verlag.

Glynn, P. W. 1993. "Coral Reef Bleaching: Ecological Perspectives." Coral Reefs 12 (1): 1–17. doi:10.1007/BF00303779.

Goreau, Thomas F. 1959. "The Ecology of Jamaican Coral Reefs I. Species Composition and Zonation."

Ecology 40 (1): 67–90. doi:10.2307/1929924.
Greenstein, B. J., H. A. Curran, and J. M. Pandolfi. 1998. “Shifting Ecological Baselines and the Demise of Acropora Cervicornis in the Western North Atlantic and Caribbean Province: A Pleistocene Perspective.” Coral Reefs 17 (3): 249–61. doi:10.1007/s003380050125.
Harmon, Russell S., Richard M. Mitterer, Nivat Kriausakul, Lynton S. Land, Henry P. Schwarcz, Peter Garrett, Grahame J. Larson, H. Leonard Vacher, and Mark Rowe. 1983. “U-Series and Amino-Acid Racemization Geochronology of Bermuda: Implications for Eustatic Sea-Level Fluctuation over the Past 250,000 Years.” Palaeogeography, Palaeoclimatology, Palaeoecology 44 (1): 41–70. doi:10.1016/0031-0182(83)90004-4.
Hönisch, B., A. Ridgwell, D. N. Schmidt, E. Thomas, S. J. Gibbs, A. Sluijs, R. Zeebe, et al. 2012. “The Geological Record of Ocean Acidification.” *Science* 335 (6072): 1058–63. doi:10.1126/science.1208277.
Jeremy B. C. Jackson. 1992. “Pleistocene Perspectives on Coral Reef Community Structure.” American Zoologist 32 (6): 719–31.
Jordan-Dahlgren, E., MA Maldonado, and RE Rodriguez-Martinez. 2005. “Diseases and Partial Mortality in Montastraea Annularis Species Complex in Reefs with Differing Environmental Conditions (NW Caribbean and Gulf of Mexico).” Diseases Of Aquatic Organisms 63 (1): 3–12. doi:10.3354/dao063003.
Kenkel, Carly D., and Mikhail V. Matz. 2016. “Gene Expression Plasticity as a Mechanism of Coral Adaptation to a Variable Environment.” *Nature Ecology & Evolution* 1 (November): 14.
Klaus, James S., and Ann F. Budd. 2003. “Comparison of Caribbean Coral Reef Communities before and after Plio-Pleistocene Faunal Turnover: Analyses of Two Dominican Republic Reef Sequences.” PALAIOS 18 (1): 3–21.
Knowlton, N., J. L. Maté, H. M. Guzmán, R. Rowan, and J. Jara. 1997. “Direct Evidence for Reproductive Isolation among the Three Species of the Montastraea Annularis Complex in Central America (Panamá and Honduras).” Marine Biology 127 (4): 705–11. doi:10.1007/s002270050061.
Knowlton, Nancy. 1992. “Thresholds and Multiple Stable States in Coral Reef Community Dynamics.” American Zoologist 32 (6): 674–82. doi:10.1093/icb/32.6.674.
Knowlton. 2001. “The Future of Coral Reefs.” Proceedings of the National Academy of Sciences 98 (10): 5419–25.
L.F. Montaggioni and C.J.R. Braithwaite, ed. 2009. “Quaternary Coral Reef Systems: History, Development Processes and Controlling Factors.” In Developments in Marine Geology, Volume 5:iii. Elsevier. http://www.sciencedirect.com/science/article/pii/S1572548009050167.
Lighty, R. G., I. G. Macintyre, and R. Stuckenrath. 1982. “*Acropora Palmata* Reef Framework: A Reliable Indicator of Sea Level in the Western Atlantic for the Past 10,000 Years.” Coral Reefs 1 (2): 125– 30. doi:10.1007/BF00301694.
Ludwig, KR, DR Muhs, KR Simmons, RB Halley, and EA Shinn. 1996. “Sea-Level Records at Similar to 80 Ka from Tectonically Stable Platforms: Florida and Bermuda.” Geology 24 (3): 211–14.
Macintyre, Ian G., Randolph B. Burke, and Robert Stuckenrath. 1977. “Thickest Recorded Holocene Reef Section, Isla Pérez Core Hole, Alacran Reef, Mexico.” Geology 5 (12): 749. doi:10.1130/0091-7613(1977)5<749:TRHRSI>2.0.CO;2.
Mann, Paul, F. W. Taylor, Kevin Burke, and Robert Kulstad. 1984. “Subaerially Exposed Holocene Coral Reef, Enriquillo Valley, Dominican Republic.” GSA Bulletin 95 (9): 1084–92. doi:10.1130/0016-7606(1984)95<1084:SEHCRE>2.0.CO;2.
Mesolella, Kenneth J., R. K. Matthews, Wallace S. Broecker, and David L. Thurber. 1969. “The Astronomical Theory of Climatic Change: Barbados Data.” The Journal of Geology 77 (3): 250–74. doi:10.1086/627434.
Mumby, Peter J., Alan Hastings, and Helen J. Edwards. 2007. “Thresholds and the Resilience of Caribbean Coral Reefs.” Nature 450 (7166): 98–101. doi:10.1038/nature06252.
Pandolfi, John M. 2007. “A New, Extinct Pleistocene Reef Coral From The Montastraea ‘Annularis’ Species Complex.” Journal of Paleontology 81 (3): 472. doi:10.1666/05046.1.
Pandolfi, John M. 2011. “The Paleoecology of Coral Reefs.” In Coral Reefs: An Ecosystem in Transition, edited by Zvy Dubinsky and Noga Stambler, 13–24. Dordrecht: Springer Netherlands.

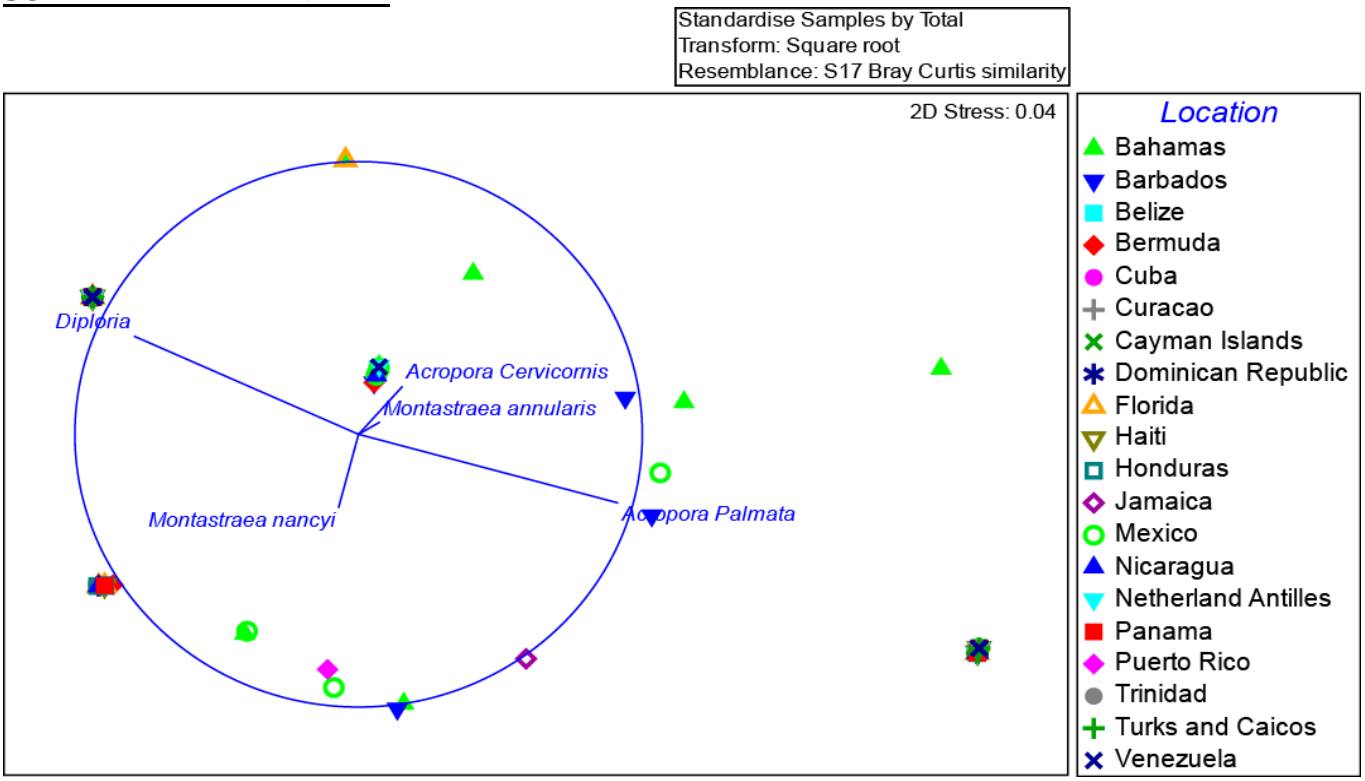
http://dx.doi.org/10.1007/978-94-007-0114-4_2.
Pandolfi, John M., and Jeremy B. C. Jackson. 2001. “Community Structure Of Pleistocene Coral Reefs Of Curaçao, Netherlands Antilles.” Ecological Monographs 71 (1): 49–67. doi:10.1890/0012-9615(2001)071[0049:CSOPCR]2.0.CO;2.
Pandolfi, John M., Catherine E. Lovelock, and Ann F. Budd. 2002. “Character Release Following Extinction In A Caribbean Reef Coral Species Complex.” Evolution 56 (3): 479–501. doi:10.1554/0014-3820(2002)056[0479:CRFEIA]2.0.CO;2.
Perry, Christopher T. 2000. “Macroboring of Pleistocene Coral Communities, Falmouth Formation, Jamaica.” PALAIOS 15 (5): 483–91. doi:10.2307/3515517.
Precht, William F., and Steven L. Miller. 2007. “Ecological Shifts along the Florida Reef Tract: The Past as a Key to the Future.” In Geological Approaches to Coral Reef Ecology, 192:237–312. New York, NY: Springer New York.
Precht, William F., Reef Resources. 1991. “Reef Facies Distribution Patterns, Pleistocene (125 Ka) Falmouth Formation, Rio Bueno, Jamaica, W.I.” AAPG Bulletin 75 (Journal Article). doi:10.1306/0C9B0B61-1710-11D7-8645000102C1865D.
Randall, C. J., and R. van Woesik. 2015. “Contemporary White-Band Disease in Caribbean Corals Driven by Climate Change.” Nature Clim. Change 5 (4): 375–79.
Reuter, M., A. Böcker, H. Lohmann, and T. C. Brachert. 2013. “The Lago Enriquillo Fringing Reef (Dominican Republic): A Unique Window into Holocene Coral Reef Ecosystems of the Caribbean Sea.” International Journal of Earth Sciences 102 (3): 781–82. doi:10.1007/s00531-013-0869-5.
Rowan, R, and N Knowlton. 1995. “Intraspecific Diversity and Ecological Zonation in Coral-Algal Symbiosis.” Proceedings of the National Academy of Sciences 92 (7): 2850–53.
Schellmann, G., and U. Radtke. 2004. “A Revised Morpho- and Chronostratigraphy of the Late and Middle Pleistocene Coral Reef Terraces on Southern Barbados (West Indies).” Earth Science Reviews 64 (3): 157–87. doi:10.1016/S0012-8252(03)00043-6.
Stathakopoulos, A., and B. M. Riegl. 2015. “Accretion History of Mid-Holocene Coral Reefs from the Southeast Florida Continental Reef Tract, USA.” Coral Reefs 34 (1): 173–87. doi:10.1007/s00338-014-1233-3.
Steinen, Randolph P., and Robert K. Matthews. 1973. “Phreatic vs. Vadose Diagenesis; Stratigraphy and Mineralogy of a Cored Borehole on Barbados, W. I.” Journal of Sedimentary Research 43 (4): 1012. doi:10.1306/74D728D8-2B21-11D7-8648000102C1865D.
Taylor, F. W., Paul Mann, S. Valastro, and Kevin Burke. 1985. “Stratigraphy and Radiocarbon Chronology of a Subaerially Exposed Holocene Coral Reef, Dominican Republic.” The Journal of Geology 93 (3): 311–32. doi:10.1086/628954.
Toscano, Marguerite A. 2016. “Revised Paleoenvironmental Analysis of the Holocene Portion of the Barbados Sea-Level Record: Cobbler’s Reef Revisited.” Coral Reefs 35 (2): 641–53. doi:10.1007/s00338-016-1397-0.
Toscano, Marguerite A., and Joyce Lundberg. 1999. “Submerged Late Pleistocene Reefs on the Tectonically-Stable S.E. Florida Margin: High-Precision Geochronology, Stratigraphy, Resolution of Substage 5a Sea-Level Elevation, and Orbital Forcing.” Quaternary Science Reviews 18 (6): 753–67. doi:10.1016/S0277-3791(98)00077-8.
Vollmer, Steven V., and Stephen R. Palumbi. 2002. “Hybridization and the Evolution of Reef Coral Diversity.” Science 296 (5575): 2023–25. doi:10.1126/science.1069524.
Weil, E., And N. Knowlton. 1994. “A Multi-Character Analysis Of The Caribbean Coral Montastraea-Annularis (Ellis And Solander, 1786) And Its 2 Sibling Species, *M-Faveolata* (Ellis And Solander, 1786) And *M-Franksi* (Gregory, 1895).” Bulletin Of Marine Science 55 (1): 151–75.
Wellington, Gerard M. 1982. “An Experimental Analysis of the Effects of Light and Zooplankton on Coral Zonation.” Oecologia 52 (3): 311–20. doi:10.1007/BF00367953.

TABLES

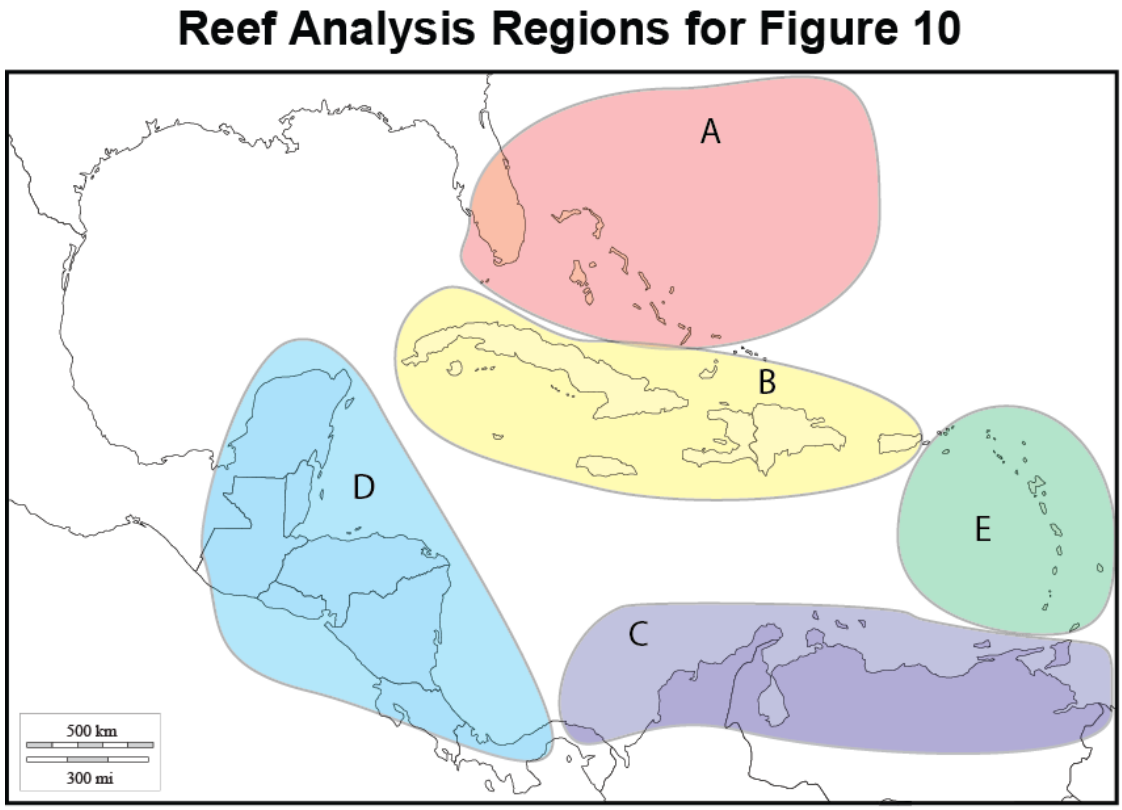
Table 1: Data collection areas for the database.

	Modern/Holocene	82 kya	125 kya	195-200 kya
Bahamas	X		X	
Barbados	X	X	X	X
Belize	X		X	
Bermuda	X	X	X	
Cayman Islands	X		X	
Cuba	X			
Curacao	X		X	
Dominican Republic	X	X	X	
Florida	X	X	X	
Guadolope	X		X	X
Haiti	X	X	X	
Honduras	X		X	
Jamaica	X		X	
Mexico	X		X	
Netherland Antillies	X		X	
Nicaragua	X		X	
Panama	X		X	
Puerto Rico	X		X	
Trinidad	X			
Venezuela	X		X	

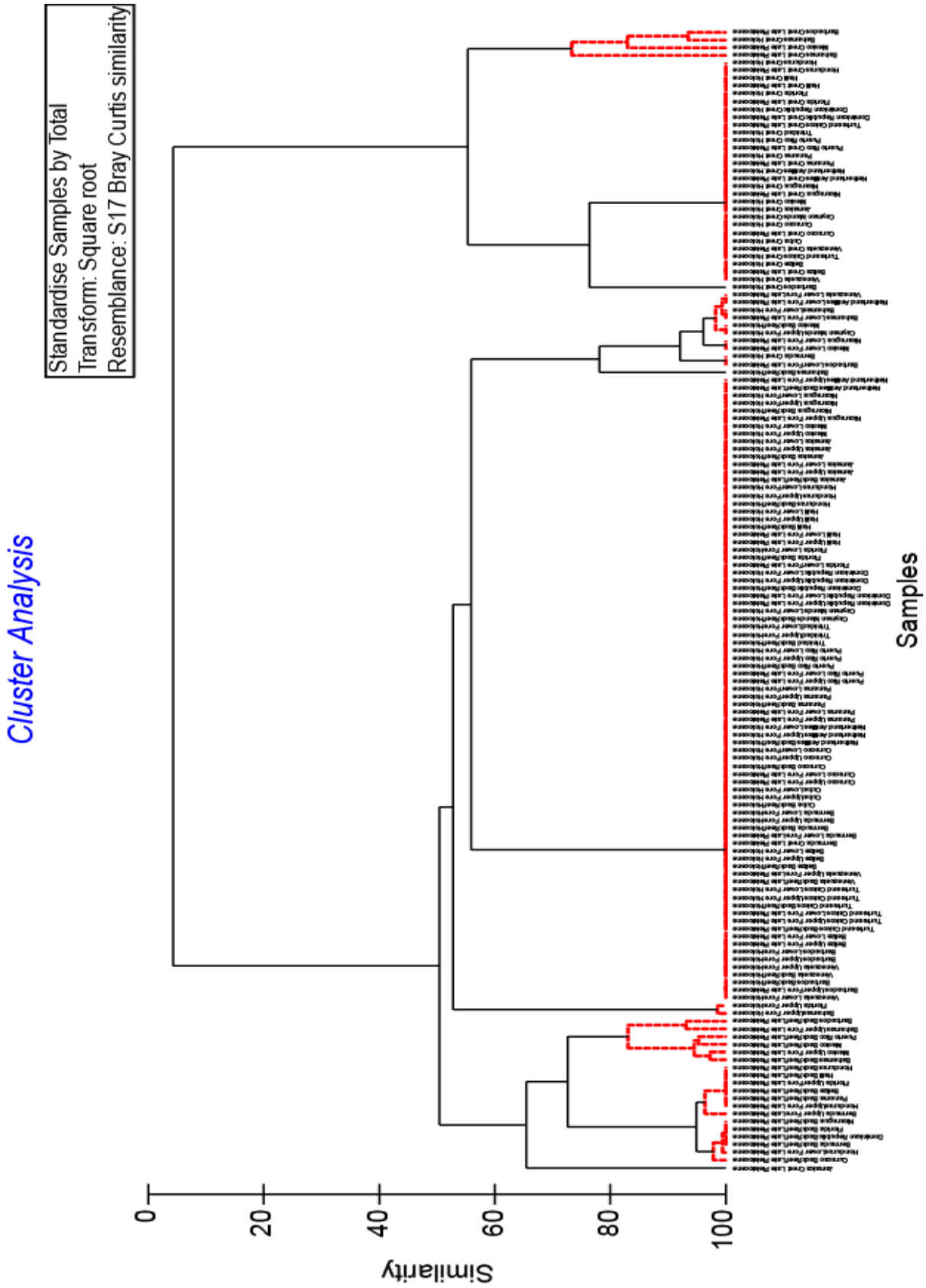
SUPPLEMENTARY DATA



Supplementary Data 2: Location plotted with coral presence



Supplementary Data 2: Caribbean Reef Regions for Figure 10



Supplementary Data 3: Cluster analysis of the database corals

About the Author:

Walker Charles Wiese is a graduate from the University of Texas at Austin with a Bachelor of Arts in Plan II Honors and History, and a Bachelor of Science in Geological Sciences. Walker was born in Chicago, IL, but moved to Texas at a young age. He graduated high school from Woodberry Forest School in 2011 at which time he decided to follow his passion for scuba diving and marine research. After many years diving and studying corals, he is excited to continue teaching and showing people the underwater world.